UNIVERSITÉ DU QUÉBEC À MONTRÉAL

UTILISATION DES CAMÉRAS DE PIÉGEAGE ET DES MODÈLES DE CAPTURE-RECAPTURE POUR L'ESTIMATION DES DENSITÉS DE CHIMPANZÉS D'AFRIQUE OCCIDENTALE (*PAN TROGLODYTES VERUS*) EN CÔTE D'IVOIRE

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RÉSUMÉ

Des estimations de densité exactes et précises sont indispensables pour évaluer les effets des menaces spécifiques sur une espèce, mesurer le succès de décisions de conservation, et pour comprendre l'écologie des populations animales. La méthode des caméras de piégeage, combinée aux modèles de capture-recapture (C-R), a récemment été mise au point pour surmonter les limitations des techniques conventionnelles d'inventaire des populations de grands singes. Cependant, aucune validation de la méthode n'a été réalisée à ce jour. Dans cette étude, je vise à valider l'utilisation de caméras de piégeage en combinaison avec les modèles de C-R pour estimer les densités de chimpanzés d'Afrique occidentale (*Pan troglodytes verus*). Plus précisément, je vise à identifier: 1) quelle est la meilleure méthode de C-R pour estimer les densités de chimpanzés par caméras de piégeage, 2) quel est l'effort de piégeage minimum requis pour des estimations de densités exactes et précises, et 3) si un placement aléatoire des caméras peut donner des mesures de densité fiables et robustes. Afin de répondre à ces trois objectifs, j'ai mené une étude de caméras de piégeage de 10 mois sur le territoire d'une communauté de chimpanzés habituée à la présence humaine, et donc où la densité totale de chimpanzés est déjà connue. Les caméras ont été placées selon deux placements différents: systématiquement, où les caméras ont été installées à chaque kilomètre, ou stratégiquement, à des endroits fréquemment visités par les chimpanzés. Les résultats montrent que tous les modèles de C-R ont donné des estimations de densité plus exactes et plus précises que les autres méthodes couramment utilisées pour le recensement des populations de grands singes. Les chimpanzés avaient deux fois plus de chances d'être filmés par les caméras placées de façon stratégique, mais les densités issues des caméras systématiques étaient aussi précises et robustes. Ainsi, cette étude met l'accent sur la pertinence des caméras de piégeage et des modèles de C-R comme outils de surveillance des populations des grands singes.

MOTS-CLÉS: caméras de piégeage, chimpanzés, *pan troglodytes verus*, suivi, densité, capture-marquage-recapture, modèles spatiaux de capture-marquage-recapture, Côte d'Ivoire.

INTRODUCTION GÉNÉRALE

État global des populations de grands singes dans le monde

En plus de la perte et de la fragmentation d'habitat causées par l'exploitation des ressources forestières, l'agriculture, et l'exploitation minière, gazière et pétrolière, la survie des grands singes sauvages est menacée par le braconnage, la capture illégale des individus à des fins récréatives ou biomédicales, les instabilités politiques, ainsi que la transmission de maladies mortelles par l'homme (Cowlishaw et Dunbar, 2000; Walsh *et al.*, 2003; Kormos *et al.*, 2004; Campbell *et al.*, 2008; Maldonaldo *et al.*, 2012).

Les baisses alarmantes des populations de grands singes en Afrique démontrent l'urgence d'instaurer des mesures de conservation drastiques pour en protéger les populations restantes (Kormos *et al.*, 2004; Campbell *et al.*, 2008; Rainer *et al.*, 2013). Au cours des trente dernières années, les populations de chimpanzés sauvages en Afrique tropicale ont diminué de plus de 66%, passant d'environ 600 000 à moins de 200 000 individus (Butynski, 2001). Par conséquent, toutes les sous-espèces de chimpanzé commun (*Pan troglodytes*), y compris le chimpanzé d'Afrique occidentale (*P. t. verus*), sont actuellement classées comme étant "en danger" (EN) par l'Union Internationale pour la Conservation de la Nature (UICN) (Oates *et al.*, 2008). Ainsi, si aucune action de conservation d'urgence n'est mise en place, les populations de chimpanzés sauvages risquent de s'éteindre au cours des prochaines années (Oates *et al.*, 2008). Au Bénin, au Togo et au Burkina Faso, les populations de chimpanzés d'Afrique occidentale se sont déjà éteintes, et les populations du Sénégal, de la Guinée-Bissau, de la Côte d'Ivoire et du Ghana restent extrêmement menacées (Butynski, 2001; Campbell *et al.*, 2008).

Pour faire face à ces menaces et mettre en place des mesures de conservation appropriées, les biologistes doivent se baser sur des données de densités des populations précises, à partir desquelles tout changement peut être facilement mesuré en permanence. Les populations de chimpanzés demeurent pourtant encore peu suivies. Les inventaires nationaux requis pour établir des stratégies de conservation à long terme restent rares, ne couvrent qu'une petite partie des populations de chimpanzés, ou ont été réalisés il y a plus d'une dizaine d'années (Kormos *et al.*, 2004; Campbell *et al.*, 2008; Maldonado *et al.*, 2012). Ainsi, afin de mieux comprendre le statut de ces populations, la réalisation d'inventaires nationaux et la mise en place de méthodes de suivi applicables à grande échelle sont devenues la priorité de plusieurs plans d'action de conservation des grands singes (Morgan *et al.*, 2011; Plumptre *et al.*, 2011; Carlsen *et al.*, 2012; Maldonaldo *et al.*, 2012; UICN et ICCN, 2012; Dunn *et al.*, 2014; UICN, 2014).

L'estimation des densités de grands singes peut toutefois s'avérer difficile dans les grandes forêts tropicales où ils vivent, les emplacements y étant souvent difficiles d'accès, la visibilité très faible, et les individus insaisissables et très mobiles. Par conséquent, déterminer le nombre de chimpanzés avec exactitude est une tâche ardue, comme le démontrent les importantes variations entre les différentes estimations d'effectifs émises au cours des derniers recensements. En Côte d'Ivoire par exemple, des recensements nationaux par Marchesi *et al.* (1995) en 1989-1990 ont résulté en une estimation de 11 676 ± 1168 chimpanzés, alors que Teleki en comptait 500 à 1000 (Teleki, 1989). Il y a donc un besoin urgent de baser les politiques de conservation sur des données qui peuvent être comparables entre différents sites et entre les différentes années de recensements.

Les approches modernes utilisées pour le suivi des populations de grands singes incluent l'inventaire des nids sur transects linéaires (Fay et Agnagna, 1992; Furuichi

et al., 1997; Kouakou *et al.*, 2009; NGoran *et al.*, 2013), l'échantillonnage génétique (Arandjelovic *et al.*, 2010; Moore et Vigilant, 2013; McCarthy *et al.*, 2015), les enregistrements audio (Heinicke *et al.*, 2015; Kalan *et al.*, 2015), et les observations directes (Mitani *et al.*, 1993; Morgan *et al.*, 2006). Bien que largement appliquées et efficaces pour l'estimation de densités, ces approches ont certaines limites pour un suivi plus approfondi, qui requiert généralement une connaissance des paramètres sociodémographiques tels que l'âge, le sexe, et l'identité des individus (Head *et al.*, 2013). De plus, ces méthodes manquent de précision pour mesurer les changements à petite échelle (Head *et al.*, 2013), dépendent de variables difficiles à mesurer (Bradley *et al.*, 2008; Kühl *et al.*, 2008; Mathewson *et al.*, 2008; Guschanski *et al.*, 2009), et sont difficiles à reproduire et à standardiser en raison d'une expérience parfois inégale des utilisateurs de la technique, des biais d'observation, et des différences dans les efforts d'échantillonnage (Ahumada *et al.*, 2013).

Avec l'arrivée des caméras numériques de piégeage au cours de la dernière décennie, de nombreux projets de recherche ont commencé à les utiliser pour l'inventaire des vertébrés terrestres, en particulier dans les habitats forestiers, où les taux de rencontre avec les moyens et grands vertébrés sont souvent faibles (Klailova *et al.*, 2012; Ahumada *et al.*, 2013; Head *et al.*, 2013; Nakashima *et al.*, 2013). Les caméras de piégeage sont un outil efficace, à haut rapport qualité/prix, et dont les résultats peuvent être facilement reproductibles (Ahumada *et al.*, 2013). En comparaison avec d'autres méthodes d'échantillonnage sur le terrain, elles sont faciles à standardiser, car l'influence humaine et l'erreur sont réduites au placement et à l'entretien des caméras, ainsi qu'à l'identification des individus filmés (Ahumada *et al.*, 2013). Si la mise en place des caméras de piégeage est conçue correctement, elles fournissent des informations très précieuses sur la communauté de vertébrés terrestres suivie, telle que la diversité des espèces, l'occupation de l'espace, l'abondance des individus, la reconnaissance des individus, la structure d'âge des groupes (mâles, femelles, juvéniles), ainsi que les budgets d'activité, les comportements, et les mouvements des

individus (Klailova *et al.*, 2012; Ahumada *et al.*, 2013; Head *et al.*, 2013). Swann *et al.* (2011) considèrent que les données acquises par caméras de piégeage sont en quelque sorte 'supérieures' à celles des observations directes, puisqu'elles peuvent être révisées par d'autres chercheurs. De plus, les résultats peuvent être reproduits sur le terrain de façon saisonnière ou annuelle, et ce pour les mêmes conditions d'échantillonnage. Enfin, un grand nombre d'études utilisant des caméras de piégeage ont porté leurs inventaires sur plusieurs espèces à la fois (Giman *et al.*, 2007; Jiménez *et al.*, 2010; Head *et al.*, 2012; Ahumada *et al.*, 2013; Head *et al.*, 2013), mettant en évidence le grand potentiel des caméras quant aux interactions entre les espèces et au suivi de la biodiversité (Burton *et al.*, 2015). Toutefois, bien que l'adoption de nouvelles technologies comme celle des caméras présente de nombreux atouts, sans le développement parallèle des méthodes d'analyses des données issues des caméras, cette technologie ne pourra être systématiquement implantée dans les programmes de biomonitoring des espèces de grands singes (Burton *et al.*, 2015).

Utilisation des caméras de piégeage en combinaison avec les modèles statistiques de capture-recapture

L'utilisation de caméras de piégeage pour l'estimation des densités des communautés animales a fait ses preuves lorsqu'elle est combinée à une approche d'analyse statistique de type Capture-Recapture (C-R) (Winarni *et al.*, 2005; Karanth *et al.*, 2006; Kelly *et al.*, 2008; Sollmann *et al.*, 2011; Blanc *et al.*, 2013; Borah *et al.*, 2013; Head *et al.*, 2013; Spehar *et al.*, 2015). Cette technique, sous sa forme la plus simple, s'appuie sur l'idée que la taille d'une population peut être estimée par la capture et le marquage des individus. La recapture de quelques individus à un moment ultérieur permet alors d'estimer le nombre d'individus dans la population, et ce en comparant la proportion d'individus recapturés (c'est à dire des individus identifiés plus d'une

fois), avec le nombre total d'individus capturés (White *et al.*, 1982). Deux conditions principales sous-tendent la théorie de C-R pour estimer l'abondance: 1) la population est démographiquement et géographiquement fermée (pas de naissances, de décès, d'immigration ou d'émigration pendant la période d'échantillonnage), 2) les individus marqués sont identifiés correctement (pas de perte des marques), et 3) la variation dans la probabilité de capture entre les individus de la population peut être modélisée. Effectuer de courtes périodes d'échantillonnage peut augmenter les chances de respecter la condition de fermeture de la population. Cependant, être capable de modéliser correctement la variation dans les probabilités de détection reste l'un des principaux défis dans le développement de modèles de C-R, toute hétérogénéité non modélisée provoquant un biais dans l'estimation de la taille de la population (White *et al.*, 1982; Burton *et al.*, 2015).

L'ensemble de modèles de C-R le plus couramment utilisé comprend des modèles où la probabilité de capture est constante, varie avec le temps, en réponse à la capture, au sein des individus, ou avec une combinaison de ces facteurs (Otis *et al.*, 1978; White *et al.*, 1982). Cependant, étant donné que la probabilité de détection dépend aussi de l'emplacement des individus, la nature spatiale des données de capture-recapture peut être utilisée pour déterminer les probabilités de capture (Borchers et Efford, 2008).

Les modèles spatialement explicites de capture-recapture (SECR) utilisent l'information de localisation des individus capturés pour modéliser leurs mouvements à l'intérieur et au-delà de la zone d'échantillonnage, et intègrent ce mouvement à l'estimation de la densité (Efford, 2004). De récentes études ont montré que lorsque les conditions de ces modèles sont satisfaites, ils peuvent donner les informations les plus fiables quant à la taille et aux tendances temporelles de la population ou de l'espèce (Ancrenaz *et al.*, 2012). Le développement des modèles SECR a pris de l'ampleur au cours des dernières années et une variété de méthodes existe à ce jour (Royle et Young, 2008; Marques *et al.*, 2012; Borchers *et al.*, 2014; Chandler et

Clark, 2014; Reich et Gardner, 2014; Royle *et al.*, 2014; Efford, 2015; Ramsey *et al.*, 2015). Ces modèles se basent sur l'indépendance et la distribution aléatoire des mouvements des individus dans la zone d'échantillonnage (Efford, 2004). Toutefois, aucune étude de validation n'a encore été réalisée avec les grands singes, il reste donc à voir s'ils peuvent être appliqués au suivi des populations de chimpanzés. Contrairement aux hypothèses qui sous-tendent les modèles SECR, les chimpanzés ne se mélangent pas au hasard dans une population, montrent un comportement territorial, et occupent des domaines vitaux bien définis (Teleki *et al.,* 1976; Mitani, 2006), suggérant qu'il y aurait une grande hétérogénéité de capture entre les individus de différentes communautés (Kühl *et al.*, 2008). Les rares études qui ont utilisées les méthodes SECR sur des populations de grands singes montrent toutefois que la méthode semble efficace dans l'estimation des densités, étant comparable aux autres méthodes utilisées couramment sur le terrain (Head *et al.*, 2012, 2013; Spehar *et al.*, 2015).

Contexte et objectifs de l'étude

Les baisses alarmantes notées lors des derniers recensements des populations de chimpanzés d'Afrique occidentale montrent qu'il est important de trouver des méthodes de suivi applicables à grande échelle afin de pouvoir guider les futures décisions de conservation, telles que la sélection et la mise en place d'aires protégées, la détermination du statut de l'espèce selon les critères de l'UICN, et l'identification des menaces qui pèsent sur sa survie. Pour ce faire, il est nécessaire d'évaluer la validité des méthodes de suivi non intrusives telles que les caméras de piégeage, qui ont montré de grandes possibilités pour le suivi des populations. Pourtant, aucune étude de ce type n'a encore été réalisée. En fait, les études portant sur la validation des méthodes de suivi des populations de grands singes restent rares. Pour les

chimpanzés, Kouakou *et al.* (2009) sont les seuls à avoir testé la validité d'une méthode de suivi courante, celle du recensement du nombre de nids fabriqués par les chimpanzés dans les arbres à chaque soir. Cependant, puisque cette méthode dépend de variables qui varient de site en site et entre les saisons, cette étude de validation ne s'applique qu'aux inventaires réalisés au Parc National Taï. Facilement applicables à grande échelle, les recensements par échantillonnage génétique sont de plus en plus utilisés pour l'évaluation des densités de grands singes. Pourtant, ici encore, aucune étude de validation sur une population suivie à long terme n'a été réalisée. Ainsi, de par le manque d'études qui comparent la méthode des caméras de piégeage à des méthodes déjà prouvées sur le terrain, et de par les nombreux avantages qui sont reliés à l'utilisation des caméras, il est essentiel de valider la méthode et les analyses statistiques qui en découlent, et ce en vue d'assurer un meilleur suivi des populations de grands singes.

L'objectif principal de mon étude consiste à valider la technique des caméras de piégeage au moyen des modèles de capture-recapture (CR) pour estimer la densité d'une communauté connue de chimpanzés d'Afrique occidentale dans le Parc National de Taï, en Côte d'Ivoire. Plus précisément, je vise à déterminer: 1) quelle est la meilleure méthode C-R pour estimer les densités de chimpanzés utilisant les caméras de piégeage, 2) quel est l'effort de piégeage optimal, et 3) si un placement aléatoire des caméras peut fournir des données suffisantes pour des estimations de densité précises et robustes. Afin de répondre à ces trois objectifs spécifiques, j'ai mené pendant 10 mois une étude au moyen de caméras de piégeage sur le territoire d'une communauté de chimpanzés habituée à la présence humaine, et où la densité totale de chimpanzés est donc déjà connue. Afin d'estimer la densité des populations de chimpanzés au moyen des données de caméras de piégeage, j'ai utilisé trois différentes approches couramment utilisées dans l'estimation de densités de populations: les courbes d'accumulation, les modèles de capture-recapture classiques, et les modèles spatialement explicites de capture-recapture. J'ai ensuite comparé leur

exactitude et leur précision afin de déterminer quelle approche est la plus appropriée pour le suivi des populations de chimpanzés. L'exactitude renvoie au biais exprimé en pourcentage de différence par rapport à la densité connue, et la précision a été mesurée au moyen de l'étendue de l'intervalle de confiance autour de la valeur moyenne des estimations de la densité. Afin d'identifier l'effort de piégeage optimal, défini comme le temps de piégeage minimum requis pour les estimations les plus exactes et les plus précises, j'ai estimé l'exactitude et la précision des estimations de densités pour différents efforts de piégeage en variant le nombre de semaines où les caméras opéraient. Enfin, afin de déterminer si un placement aléatoire des caméras pouvait donner des mesures de densité fiables, j'ai estimé la densité des chimpanzés à partir de données issues de caméras placées de façon systématique (à chaque kilomètre sur une grille de 1 x 1 km^2), puis comparé les probabilités de capture sous ce placement avec celles des caméras placées à des endroits fréquemment visités par les chimpanzés.

CHAPITRE I

VALIDATING THE USE OF CAMERA TRAPPING AND CAPTURE-RECAPTURE MODELS TO ESTIMATE DENSITIES OF THE ENDANGERED WESTERN CHIMPANZEE (*PAN TROGLODYTES VERUS*) IN TAÏ NATIONAL PARK, IVORY COAST

1. 1. ABSTRACT

Accurate density estimates are essential to assess the effects of specific threats, measure the success of management decisions, and understand the ecology of primate populations. As a result, great ape conservation and ecology demands a good understanding of demographic trends, density, and distribution of great ape populations. Camera trapping combined with capture-recapture (C-R) modeling has recently been developed to overcome past limitations of great ape population assessment techniques, possibly increasing the efficiency in density estimation. However, no validation of the method has yet been done with great apes. The three main objectives of this study were to identify: 1) what was the best C-R method to estimate chimpanzee densities using camera traps, 2) what was the optimal trapping effort, defined as the minimum trapping time required for the less biased and most precise estimates, and 3) whether a systematic grid of traps randomly located within the study area could provide sufficient data for robust abundance and density estimates. In order to address these three objectives, a 10-month camera trapping study was conducted on the territory of a habituated chimpanzee community, where total chimpanzee density is already known. Three commonly used approaches to

estimate density were compared: accumulation curves, conventional capture-recapture models, and spatially explicit capture-recapture models (SECR). Cameras were placed according to two different camera placements: a systematic one, where cameras were placed every kilometer, and a targeted one, where cameras were placed at locations frequently visited by chimpanzees. Effective sampling area (ESA) was calculated using tracking data from at least one focal individual combined over 174 days throughout 2013-2015, and all members of the community were followed at least once. The results show that all three methods gave accurate and precise density estimates that were generally comparable with one another (i.e. overlapping 95% CIs). Estimates from CAPTURE and MARK were the most accurate, and densities estimated by accumulation curve techniques were always less accurate than the other methods. Within each method (except accumulation curves), there was no significant variation between estimates from the model that did not consider heterogeneity in capture probability and estimates from the models that did. This suggests that heterogeneity in capture probability was minor. I propose that SECR models should be used to estimate chimpanzee densities via camera traps. The results show that the method is more accurate and more precise than other census methods commonly used to census great ape populations. At last, the results have shown that detection probabilities are highest under a targeted placement, but that a systematic layout still yields accurate estimates. This study thereby emphasizes the suitability of combining C-R and SECR modeling and camera trapping as useful monitoring tools for great ape conservation and ecology.

1.2. INTRODUCTION

For conservation management to be effective on the long term, researchers need to obtain accurate census data from which change can be easily and continuously measured. However, in large rainforests, estimating great ape densities can be difficult as locations can be hard to access, visibility is very low, and individuals are elusive and highly mobile. As a result, indirect methods such as nest or dung counts are most often used to estimate population densities (Anderson *et al.*, 1983; Blom *et al.*, 2001; Dupain *et al.*, 2004; Devos *et al.*, 2008; Kühl *et al.*, 2008; Todd *et al.*, 2008; Kouakou *et al.*, 2009; Granier *et al.*, 2014). Yet, fixed relationships between nest numbers or dung piles and great ape densities do not exist, as both nest decay or dung production rates need to be known, and have been found to vary between field sites, climates, seasons, and individuals (Kühl *et al.*, 2008; Mathewson *et al.*, 2008; Todd *et al.*, 2008). Data collection for these variables requires considerable investment of time and effort, and thus their values mostly remain unknown across sites (Todd *et al.*, 2008; Kouakou *et al.*, 2009; Spehar *et al.*, 2015). Imprecision and bias of density estimates from indirect signs may also be created by inter-observer error, low encounter rates, and nest reuse and production rates (Bradley *et al.*, 2008; Kühl *et al.*, 2008; Guschanski *et al.*, 2009).

In order to overcome these difficulties, population assessment technologies in conjunction with advances in capture-recapture modeling have been developed (Arandjelovic *et al.*, 2010; Moore and Vigilant, 2013; Head *et al.*, 2013; Roy *et al.*, 2014; Spehar *et al.*, 2015). These require a set of detectors to be deployed in which individuals from an animal population can be directly or indirectly captured, marked and released. In its simplest form, population size can then be inferred by calculating the proportion of individuals already marked when caught at another occasion (White *et al.*, 1982). Detectors can take various forms: physical traps (Borchers and Efford, 2008; Gerber and Parmenter, 2015), acoustic devices (Efford *et al.*, 2009*a*; Marques

et al., 2012), hair snares (Howe *et al.*, 2013), but area searches for fecal samples (Arandjelovic *et al.*, 2010; Moore and Vigilant, 2013; Roy *et al.*, 2014; McCarthy *et al.*, 2015) and camera traps (Head *et al.*, 2013; Spehar *et al.*, 2015) have been the types of detectors most extensively used with great apes. Genetic censuses via collection of fecal samples have shown more accurate results than nest counts, but individuals can be missed in sweeps, and the method remains to be validated on a known population (Arandjelovic *et al.*, 2010; Roy *et al.*, 2014; McCarthy *et al.*, 2015).

The use of camera traps with capture-recapture (C-R) statistical analysis has proven successful for density estimation in several surveys of large mammal species (Karanth and Nichols, 1998; Kelly *et al.*, 2008; Royle *et al.*, 2011; Gray and Prum, 2012; Noss *et al.*, 2012; Sollmann *et al.*, 2012; Weingarth *et al.*, 2012; Borah *et al.*, 2013; Tobler *et al.*, 2013), including great apes (Head *et al.*, 2013; Spehar *et al.*, 2015). Camera traps have shown higher species detection rates (Bowkett *et al.*, 2006), and are able to take records of the most elusive and rare species (Carbone *et al.*, 2001; Pettorelli *et al.*, 2009). When individuals can be distinguished from one another, individual-level data can be obtained, and this with relatively low effort (Head *et al.*, 2013; Boyer-Ontl and Pruetz, 2014). Two main assumptions underlie C-R theory: 1) the population is demographically and geographically closed (i.e., no births, deaths, immigration or emigration throughout the sampling period); and 2) variation in capture probability can be accounted for. Ensuring sampling periods are short enough can increase chances that the assumption of population closure will be met. However, being able to correctly model variation in individual detection probabilities has remained one of the main challenges in the development of capture-recapture models, all unmodeled individual heterogeneity causing biases in the estimation of population size (White *et al.*, 1982; Burton *et al.*, 2015).

The most commonly used set of capture-recapture models are those elaborated by Otis *et al.* (1978), which were further implemented in computer programs such as

CAPTURE (White *et al.*, 1978) and MARK (White and Burnham, 1999). This set includes models where capture probability is constant (M_o), varies with time (M_t), with behavioural response to capture (M_b), among individuals (M_h), or with a combination of these factors (M_{th}, M_{tb}, M_{tbh}) (White *et al.*, 1982).

However, since probability of detection also depends on the location of animals, the spatial nature of the capture-recapture data can be used to determine capture probability (Borchers and Efford, 2008). Spatially explicit capture-recapture models (SECR) include the location of detections from capture-recapture studies and are therefore able to model the variation in exposure to detectors of animals whose activity centers are distributed throughout the sampled habitat (Efford and Mowat, 2014). SECR models can also incorporate other sources of variation in capture probability, such as sexual and individual differences in ranging patterns (Sollmann *et al.*, 2011; Tobler *et al.*, 2013). Yet, their validity for density estimation of gregarious and territorial species like chimpanzees remains to be tested using camera traps.

SECR models are based on the assumption that individuals move independently and are randomly distributed across the sampling area (Efford, 2004). Chimpanzees do not mix randomly within a population, show territorial behaviour, and occupy defined home ranges (Teleki *et al.*, 1976; Mitani, 2006), suggesting that there would be large capture heterogeneity between individuals (Kühl *et al.*, 2008). No standardized method has yet been developed to estimate chimpanzee densities via camera traps and C-R models, and thus further assessments and developments are needed before the method can be used to guide management and conservation decisions (Kühl *et al.*, 2008).

From 1995 to 2007, the population size of western chimpanzees (*Pan troglodytes verus*) living in Côte d'Ivoire declined by an alarming 90%, a country which remains to be thought of as one of the final refuge for this subspecies (Campbell *et al.*, 2008).

Taï National Park (TNP) in South Western Côte d'Ivoire harbours long-term research sites on chimpanzee behaviour and ecology (Campbell *et al.*, 2008; N'Goran *et al.*, 2013). Four chimpanzee communities living in the park have gradually been habituated to human presence since the 1980s (Boesch and Boesch-Achermann, 2000), and thus offer a unique opportunity to validate approaches used to estimate densities from capture-recapture models using camera trap data.

The overall goal of my study was to validate the use of camera trapping in combination with capture-recapture models to estimate the density of a habituated community of western chimpanzees in Taï National Park, Ivory Coast. More specifically, I aimed to identify: 1) what the best C-R method to estimate chimpanzee densities is using camera traps, 2) what the optimal trapping effort is, and 3) whether a systematic grid of traps randomly located within the study area could provide sufficient data for robust abundance and density estimates. In order to address these three objectives, I conducted a 10-month camera trapping study on the territory of a habituated chimpanzee community, where chimpanzee total density is already known. I calculated density estimates from camera trap data using three commonly used density estimation approaches: accumulation curves, closed capture-recapture models in CAPTURE and MARK, and spatially explicit capture-recapture models, and then compared their accuracy and precision. Accuracy was defined as the percentage of bias from the known density, and precision as a measure of the confidence interval width. In order to identify the optimal trapping effort, defined as the minimum trapping time required for the less biased and most precise estimates, I estimated accuracy and precision of density estimates for various numbers of camera trapping weeks (i.e. number of occasions). At last, I calculated density separately for each camera trap layout and assessed whether accuracy and precision of estimates under the systematic layout were high, and compared detection probabilities for each layout, in order to see whether a systematic layout of cameras could be used to monitor chimpanzee populations.

1.3. METHODS

1.3.1. Study site and subjects

The study was conducted from June 2014 to March 2015 (total of 273 days) in Taï National Park, Ivory Coast (5°08'N to 6°407'N, and 6°47'W to 7°25'W). Average annual rainfall in the study area is approximately 1800 mm and annual average temperature between 24 and 30°C (Anderson *et al.*, 2005). In the eastern part of the park, a chimpanzee community (called the "East community") has gradually been habituated to human presence and followed on a daily basis since the 1980s by researchers and assistants of the Taï Chimpanzee Project (TCP) (Figure 1.1) (Boesch and Boesch-Achermann, 2000).

Tracking data from 2013 to 2015 (total of 154 days) of at least one focal individual per day of the east community was used to calculate the 95% fixed kernel density estimate of community territory size, using the Geographic Information System software ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, USA), with the extension module Hawths Tools (Beyer, 2004). This resulted in an estimated area of 40.37 km^2, hereafter considered as the "effective sampling area" (ESA). Focal follows of members from the east community carried out simultaneously as the camera trapping survey allowed knowing that, throughout the study period, the community was composed of a total of 36 individuals. Of these, an adult female and her infant disappeared, one juvenile was found dead, and two subadult females were seen leaving the group and coming back throughout the sampling period, although the last two individuals remained in the community for most of the duration of the study period. These closure violations will be discussed in the appropriate section of the discussion. Known density of the effective sampling area was thus calculated as 0.89 ind/km^2 (D=36/40.37 km^2).

1.3.2. Camera trap layout

A total of 81 (mean: 64, range: 13-81) cameras (Bushnell Trophy Cam™; http://bushnell.com) were deployed over the 10-month period across an area of 42 km^2 (figure 1.2). Using a grid of cells 1x1 km^2 that overlapped the territory of the east community, I placed cameras according to two layouts: a systematic (total of 23 cameras) and a targeted layout (58 cameras). Systematic cameras were placed at the intersections of cells in the core of the territory, within 30 meters of the point given by the GPS, and oriented towards the geographic north. Within each cell, targeted cameras were installed at locations frequently visited by chimpanzees, with a maximum of two cameras per cell. These locations included potential tool use sites (i.e. nut cracking sites, army ants nests), small water holes, natural bridges, fruiting trees, and trails. All cameras were placed between 0.3 (ex: nut cracking sites) to 1.6 meters (ex: natural bridges) above the ground. All cameras were set to a high sensitivity. Motion detectors were programmed to trigger as soon as movement was detected, and were active 24 hours a day. Videos were recorded for a period of 60 seconds. In cases where individuals were in front of the camera for several minutes, continuous 60s videos were recorded with an interval of minimum one second. Cameras recorded date and time at which individuals were filmed. All cameras were visited once or twice a month, and batteries, silica gel, SD cards and cling film protecting the cameras were changed. The targeted placement aimed to increase the probability of filming individuals, and thus, when the data on SD cards showed that no chimpanzee was filmed within the last month; targeted cameras were moved to another targeted location within the same cell. This resulted in a total of 103 camera locations for the targeted placement (Figure 1.2). Systematic cameras were never moved and thus remained at the same locations throughout the entire study period.

1.3.3. Data collection

For each video that recorded a chimpanzee, I noted the date and time of the video, the GPS location of the camera, as well as the identity of the chimpanzees that were filmed. Capture histories were calculated for each individual for a total of 39 trapping occasions, where one occasion represented seven consecutive camera trapping days (total of 273 days). Systematic cameras were installed one week prior to the targeted cameras, which were thus only active for 38 trapping occasions. Two experienced observers, who knew the chimpanzees and followed them on a daily basis throughout the study period, identified the chimpanzees that were filmed. Individuals were identified through a combination of facial and bodily characteristics, such as presence of scars, shape and coloration of ears, nose, face, and body (see example in figure 1.3) (Goodall, 1988). Due to lack of time, only 25% of videos could be identified by both observers, and thus data used to construct capture histories included identifications made by either of the observers (observer 1: 48 % of all videos, observer 2: 52 %), and identifications where both observers agreed, for those cases where both observers identified the chimpanzees. This resulted in a total of 1281 of 1674 (targeted) and 278 of 364 (systematic) positive identifications. Interobserver reliability was measured via Cohen's Kappa coefficient (Cohen, 1960) using the *kappa2* function of the 'irr' package (Gamer et al., 2012) in R (version 3.2.1; R Core Team, 2015).

1.3.4. Density estimation

In order to determine which C-R method gives the most accurate and precise density estimates, I compared three commonly used approaches to estimate density: (i.) accumulation curves, (ii.) conventional capture-recapture models, and (iii.) spatially explicit capture-recapture models (table 1.1).

i. Accumulation curves

First, I fitted the capture-recapture data with three different accumulation curve functions commonly used in genetic studies (Eggert *et al.*, 2003; Bellemain *et al.*, 2005; Lukacs and Burnham, 2005; Petit and Valiere, 2005). Adapted to camera trap data, the curves of the functions are determined by the accumulation of unique individuals filmed, the asymptotes representing the estimated population sizes. First, I estimated population size as Kohn *et al.* (1999) used to estimate the number of coyotes (*Canis latrans*) in California. Kohn's *et al.* function (hereafter "Kohn estimator ") assumes an accumulation curve of hyperbolic form and is given by:

$$E(x) = \frac{ax}{(b+x)}$$

where x is the number of individuals filmed, $E(x)$ the cumulative number of unique individuals filmed, a the asymptote of the function, and b the nonlinear slope of the function which declines as x increases. The second accumulation curve method ("Eggert estimator ") I tested has previously been used to estimate forest elephant (*Loxodonta cyclotis*) densities in Ghana (Eggert *et al.*, 2003), and assumes an exponential form of the accumulation curve. It is given by: $E(x) = a(1 - e^{(bx)})$. The last method was the "Bortz estimator", which also assumes a curve of exponential form, and is given by: $E(x) = a + bc^x$ (Bortz *et al.*, 1990). For each method, the capture histories were bootstrapped 1000 times to estimate the confidence intervals of a. In order to estimate density and its precision, I divided population size, SEs, and CI_u and CI_l (upper and lower 95% confidence intervals limits) by total sampling area (40.37 km^2).

ii. Capture-Recapture Models

I tested population closure in CAPTURE (White *et al.*, 1978), a test that is based on the number of occasions between the first and last captures of individuals captured twice or more (Otis *et al.*, 1978). I then calculated population size using the computer programs CAPTURE and MARK (White and Burnham, 1999). CAPTURE (available online at: http://www.mbr-pwrc.usgs.gov/software/capture.html) includes models for closed populations where capture probabilities are constant (M_o), vary with time (M_t), with behavioural response to capture (M_b), within individuals (M_h) or with a combination of these factors (M_{th}, M_{tb}, M_{tbh}) (White *et al.*, 1982) (table 1.1). Population sizes in MARK (http://warnercnr.colostate.edu/~gwhite/mark/mark.htm) are obtained with the original Otis *et al.* (1978) models (similar to CAPTURE), as well as with two-finite mixture models (Lukacs, 2015). Models in MARK were constructed using the "Closed captures", "Closed Captures with Het.", and *t*, *b*, and *h* parameterizations, by controlling for variations in initial capture probability and recapture probabilities using the Parameter Index Matrices (PIMs) (table 1.1) (White, 2008; Lukacs, 2015). Estimates of population size from these two programs were then used to estimate density by dividing population size, SEs and 95% confidence intervals by total sampling area.

iii. Spatially Explicit Capture Recapture Models

SECR models include data on the location of detectors, and fit two different models to the spatial detection histories: a spatial model of the population and a spatial model of the detection process. The first describes the distribution of home ranges centers (or activity centers (ACs)) of the individuals from the sampled population, while the other relates the probability of detecting an individual according to the distance from

each animal's activity center from the detector (Efford, 2015). In the latter, capture probabilities *p* from the conventional C-R models are replaced by a vector of at least two parameters: g_o, the probability of detection at the activity center of an animal, and σ, the spatial scale over which capture probability declines (Efford, 2004). I fitted 8 different models (table 1.1) according to variations of effects on g_o and σ, using the 'secr' 2.9 package (Efford, 2015) in R 3.0.1 (R Core Team, 2013). The *nullmodelt* assumed no effect on g_o and σ, the *tmodel* that g_o varied with time, the *bmodel* that g_o varied with behavioural response to capture, the *hmodel* that g_o and σ varied within individuals, *hsex* that g_o and σ varied according to sex, *hage* that g_o and σ varied according to age (adult, sub adult, juvenile, infant), and, at last, the *bkmodel*, a trap-specific behavioural model with effects on g_o. Days where cameras were not functioning where accounted for in all models except in the *nullmodel*, which assumed no effect on g_o and σ and no variation in trapping effort. All models assumed a Poisson distribution of activity centers and a half normal detection function. In order to estimate density, SECR evaluates the likelihood by summing values at points on a 'habitat mask', where each point represents a grid cell of potentially occupied habitat. Masks may be constructed using several approaches, such as using GPS data, or automatically generated buffers of arbitrary width placed around the detectors (Efford, 2015). To test how the choice of habitat mask has on SECR estimates, I first fitted models with a habitat mask created with the tracking data ("polygon" type in 'secr'). Then, I used the function *mask.check* from the 'secr' package to construct masks of varying buffer width and spacing. These masks are restricted to the points within a given buffer distance of any camera ("trapbuffer" type). To see which trapbuffer width gives the most accurate and precise density estimation, I tested buffer sizes 100, 500, 1000, 2000 and 5000 meters. At last, I used the function *suggest.buffer* (with a relative bias target of 0.001), which determines a suitable trapbuffer width, to see if the outcome of this function corresponds to the appropriate buffer size in *mask.check*.

1.3.4.1. Accuracy and precision of density estimates

Models from each method were compared using estimates of accuracy and precision. Accuracy was calculated using the percentage of bias, as: %Bias= ((0.89-*D*)/0.89)•100, where 0.89 ind/km^2 is the known density, and *D* the density estimated by each model. Precision was calculated as the percentage of the confidence interval width, as: %CI= ((CI_u-CI_l)/*D*) •100, where CI_u and CI_l are the upper and lower 95% confidence intervals values. As they are defined, an increasing percent bias and percent CI suggest an increasingly accurate and precise method. I selected appropriate models and estimators based on accuracy and precision, but accuracy was more important in model selection.

1.3.5. Optimal trapping effort

Optimal trapping effort, defined as the minimal effort required for the most accurate and precise density estimates, was determined by comparing density estimates for various trapping occasions (10, 20, 30 and 38 (targeted) and 39 (systematic) weeks).

1.3.6. Systematic camera trap placement

Density was calculated separately for each camera trap layout. Since both layouts did not involve the same number of camera traps, accuracy and precision of density estimates cannot be compared between both layouts. However, SECR models including trap covariates offer the possibility of calculating trap-specific detection probabilities (Efford, 2015). As a result, trap-specific initial detection probabilities (g0) from SECR models were compared between both layouts in order to see which

layout yielded higher detection probabilities.

1.4. RESULTS

For a total of 39 sampling occasions of 7 days each, 595 videos of chimpanzees were recorded, of which 514 were taken under the targeted placement and 81 under the systematic one. Up to 36 unique individuals were filmed, and thus all individuals of the group were filmed at least once. Mean capture frequency was of 6 captures (range 0-10) for the systematic placement and 16 (range 1-25) for the targeted placement. Considering only adults, males had similar capture frequencies for both the systematic (mean: 8.6, range: 6-10, as opposed to 6.89, range: 4-10 for females) and the targeted (mean: 21.6, range: 17-25, females: mean: 15.9, range: 13-22) layouts. Adults (systematic: mean: 7.5, range: 4-10; targeted: mean: 17.9, range: 16-25) had slightly higher capture frequencies than subadults, juveniles and infants (systematic: mean: 6.73, range: 1-10; targeted: mean: 16.8, range: 10-25) (see appendix I for individual capture frequencies).

1.4.1. Density estimation

Closure tests in CAPTURE for both systematic ($p<0.001$) and targeted ($p<0.001$) data showed closure violation. This was indeed the case since three individuals disappeared and two individuals temporarily left the group during the study period. Still, density estimation remained precise and accurate for most methods. Models with most accurate density estimates and related CIs for each method are shown in figure 1.4. Except estimates from MARK under the systematic layout, all models

included the true density within their 95% confidence intervals. Estimates from CAPTURE and MARK were the most accurate in both layouts, and densities estimated by accumulation curve techniques were always less accurate than the other methods. SECR estimates had the highest %CI, not going lower than 66.5% (fig. 1.4; table 1.2). Models selected according to variation in p, as well as estimates of D of MARK and CAPTURE, varied only under the systematic layout. Within each method (except accumulation curves), there was small variation between estimates from the model selected as most accurate and estimates from the M_0 model, suggesting minor heterogeneity in capture probability (see appendix II for estimates from all models).

Density estimates varied significantly between buffer size for both layouts, density decreasing with buffer size, and that only a buffer size of 1 km under the targeted placement resulted in accurate estimation of density (Effective sampling area: 40.5 km^2; *D:* 0.892 ind/km^2; SE: 1.49 ind/km^2, appendix III). Bias remained high using the 1 km buffer on data from the systematic placement (ESA: 31.7 km^2; *D*: 1.07 ind/km^2; 1.85 ind/km^2). Precision of these estimates is lower than using a polygon mask from tracking data to construct the habitat mask (table 1.2). The buffer proposed by the *suggest.buffer* function for both designs did not correspond to the appropriate buffer width given by the *mask.check* function (suggested buffers were 3693 meters for the systematic placement, and 3978 meters for the targeted).

1.4.2. Optimal trapping effort

Test of population closure showed that the assumption was met only for occasion numbers 10 and 20 under the systematic layout. Still, precision and accuracy increased with sampling occasions in both layouts (table 1.2). The number of unique individuals stabilized earlier in the targeted (at 20 occasions) than in the systematic (30 occasions) placement (figure 1.5), suggesting that optimal trapping effort is smaller under the targeted layout. Similarly, table 1.2 shows that precision and bias

reach a plateau around 20 occasions under the targeted layout, and slightly later, at 30 occasions, for the systematic layout. Precision and accuracy of estimates at 39 occasions under the systematic layout were similar to those at 10 occasions under the targeted layout.

1.4.3. Systematic layout

All 36 members of the community were filmed under the targeted placement, whereas under the systematic placement, two individuals (a female and her infant) were not filmed. Since both individuals disappeared at the beginning of the study, more effort (i.e. more sampling occasions) would not have increased chances of filming them. The targeted trap layout also yielded higher detection probabilities than the systematic one. Average initial detection probabilities (g0) across all individuals, traps, and occasions estimated from null SECR models were 0.024 at targeted and 0.010 at systematic traps, indicating that overall, targeted traps were more than twice as likely to detect chimpanzees. CR estimates of detection probability (p) from targeted and systematic arrays cannot be compared directly because they are specific to the array of traps rather than individual traps, and more targeted traps were deployed (mean numbers of traps operating per occasion were 45.26 for targeted and 19.49 for systematic layouts (ratio = 2.32)). Still, accuracy and precision after 38 occasions under the systematic layout were high (table 1.2).

1.5. DISCUSSION

1.5.1. Density estimation

To my knowledge, this is the first study validating the use of capture-recapture models and camera trapping for the density estimation of a habituated great ape community. My results show that accumulation curves, conventional capture-recapture and spatially explicit capture-recapture models gave accurate and precise density estimates that were generally comparable with one another (i.e. overlapping 95% CIs). Still, accumulation curves constantly under- or overestimated density. Whereas the method does not account for any variation in capture probabilities (Gotelli and Graves, 1996), conventional C-R and SECR models include heterogeneity of a variety of factors and thus allow for better modeling of detection probabilities, which is crucial for accurate density estimation.

There were no significant differences between the capture-recapture models that considered various sources of heterogeneity in capture probability (M_h, M_t, *bkmodel*, etc.) and the null models (M_o, *nullmodel,* etc.), which did not consider any variation, revealing that capture heterogeneity was minor. In CAPTURE, Chao's estimators (1988, 1989) were the most accurate. These were designed for sparse data (Chao, 1989), and are the most robust to non-independence of captures (Boulanger *et al.*, 2004).

C-R estimates were accurate and precise although assumption of population closure was not met throughout the study period. This might be due to the high number of recaptures for most individuals found in the study area. Studies with lower number of recaptures should therefore be cautious when using closed population models on open populations. Nevertheless, precise and accurate density estimates from open populations have also been noted in the past (Head *et al.*, 2013), and thus relaxation

of this assumption seems to be possible when sampling effort is high.

1.5.1.1. Validating the use of SECR models for chimpanzee density estimation and its implications for future model developments

Spatially explicit capture-recapture models address many of the limitations of traditional capture-recapture models, but they are based on a set of assumptions hard to be met when used with chimpanzees. SECR models were developed for solitary and non-territorial species, and thus assume independent and randomly distributed activity centers (ACs) (Efford, 2004). This is not the case in chimpanzees, since they form social groups ranging from a few individuals to more than 150 (and thus ACs are not independent), and exhibit territorial behaviour (ACs are not randomly distributed) (Teleki *et al.*, 1976; Mitani, 2006). Furthermore, since the study was done on the territory of one community of chimpanzees, the ACs of individuals were not distributed homogeneously throughout the sampling area as the SECR models assumed they did: rather, individual ranges overlapped and activity centers were clustered around the middle of the sampling area. As a result, all sampled individuals had an equal probability of detection, since their ACs were centered around the same location. Still, as my results have shown, the violation of these SECR assumptions has not affected the accuracy of the estimates, as reflected by their low %Bias.

Similarly, using multi-catch traps, Efford *et al.* (2009*b*) note that SECR estimates were robust to the failure of assumptions of independence and uniformity of ACs. As Royle *et al.* (2014) explain, assuming a homogeneous distribution of ACs still permits for infinite possible distributions of points without violating the assumption of spatial randomness. Independent, uniform points will almost never seem regularly or systematically distributed. Given that capture rates are high, the spatial randomness assumption will even have very little effect on the calculated locations of ACs, since

the uniform distribution hypothesis is only assumed *a priori*. SECR models include the spatial information of at least some individuals of the population in their density estimation, and thus their robustness is directly affected by the quantity and quality of the collected data. As a result, the bias potentially caused by violating the assumptions decreases as the total captures and individual capture frequencies increase, stressing the importance of effective sampling effort.

Estimates of chimpanzee densities from SECR were the less precise, exhibiting a minimum %CI of 66.5%. SECR models include the spatial variation of the distribution of individuals in the variance of their density estimates, and thus standard errors and confidence intervals are often higher with this method then with conventional C-R models (Obbard *et al.*, 2010; Gerber and Parmenter, 2015). As a result, they are able to include more sources of variation in capture probabilities, an important feature that is ignored in conventional capture-recapture models (Obbard *et al.*, 2010).

At a first glance, a precision of 66.5% may seem high, but comparisons with other studies that tested census approaches on great apes show that the density estimates obtained via camera trap data and SECR models were most often more precise and more accurate than those obtained via other methods. In Taï National Park, Kouakou *et al.* (2009) conducted a 12-month study on the validation of several nest count methods to census chimpanzees from three of the habituated communities in the park. Estimates of abundance were less precise (%CI of 102 to 121%), and less accurate (%Bias of 5.4 to 97.3%) than the estimates obtained from camera trap data. Kouakou *et al.* (2009) being the only other study validating a census approach on a habituated great ape population, accuracy of the density estimates from this study cannot be compared with other census methods. However, precision can be compared with other recent censuses done on great ape populations. Genetic sampling seems to yield more precision in density estimation: recently, Roy *et al.* (2014) estimated mountain

gorillas (*Gorilla beringei beringei*) abundance in Uganda using genetic capture-recapture techniques and found an estimate precision (%CI) of 20.7%. True density was unknown, but the authors reported that the method seemed to downwardly bias the minimum abundance estimate, as an important proportion of groups and individuals were missed in either of the two sweeps realized. Combining spatially explicit capture-recapture modelling with genetic sampling, McCarthy *et al.* (2015) had similar values of precision (%CI of 21.6%) for their abundance estimates of eastern chimpanzee in population size in fragmented habitat in Uganda. However, with chimpanzees in Tanzania, Moore and Vigilant (2014) had less precise results in density estimation through SECR and genetic sampling (%CI of 88%). Precision of census estimates thus seems to vary between studies, but Head *et al.* (2013) and Spehar *et al.* (2015) also noted that their SECR estimates from camera trap data were more precise than those from nest counts and genetic sampling.

Nevertheless, I have also shown that the use of telemetry data to estimate effective sampling area was crucial for accurate density estimates in SECR. When conservation managers do not have access to tracking data, the 'secr' package offers the option of calculating effective sampling area by adding a buffer strip around the detectors (i.e. cameras) (Efford, 2015). Testing various buffer widths showed that densities varied significantly with buffer size, density decreasing with increasing buffer size, and that only a buffer of 1 km resulted in accurate density estimates. This is likely due to the fact that the sampling area covered the territory of only one community of chimpanzees. Since chimpanzees are territorial, probability of detecting individuals drastically drops at a given distance from the detectors, contrarily to the binomial distribution expected by the model. As a result, I suggest that future camera trapping studies on great apes should extend sampling area over the home ranges of several communities.

SECR models are especially of interest in conservation ecology because they can be used to study a variety of ecological processes, such as landscape connectivity (Sutherland *et al.*, 2015), response to specific threats (Christiansen *et al.*, 2014; Pirotta *et al.*, 2014), and spatial variation in density (Efford *et al.*, 2009*a*). These implications extend and increase the applicability and value of capture-recapture theory for research on animal populations.

However, while this study validated the use of SECR despite violation of its core assumptions, there is still a need for future model development to account for biological and behavioral processes, such as attractive and repulsive interactions among individuals caused by territoriality and sociality. Very little research has been done on this topic. Reich and Gardner (2014) have been the first to propose a model that accounts for a spatial variation in density and potential repulsive interactions between individuals' activity centers, but it is only applicable to solitary species. The validity of SECR modelling for group living species thus remains to be tested with other gregarious and territorial species. Future studies should also focus on sampling larger areas, which are covered by several communities of chimpanzees, so that sampled individuals do not have equal probability of capture according to the locations of their activity centers. Camera trap array should thus be greater than the home ranges of chimpanzee communities of the study area. Albeit these limitations, I suggest that SECR models are chosen to estimate chimpanzee densities with camera traps, since they offer accurate results and include more sources of variation in their precision then conventional capture-recapture models. This is an important feature that should be considered in future censuses of great ape populations, since conservation management needs to include all possible sources of uncertainty in the data used to make conservation decisions.

1.5.2. Optimal trapping effort

The results have shown that increasing the number of occasions will increase both accuracy and precision of density estimates. Comparing estimates from various occasion numbers has shown that under a targeted placement, a minimum survey period of 20 weeks is required, if encounter rates are similar to the ones from this study. This period should be longer in case of a systematic placement, which required 30 to 40 weeks for good density estimation.

1.5.3. Systematic layout

Heterogeneity in capture probability between individuals remains a challenge in density estimation because it is difficult to identify all sources of variation and to model them appropriately. Therefore, the best option is to simply remove the effects of heterogeneity by increasing the chances that most individuals of the population will be caught several times (Gerber and Parmenter, 2015). With this study, I have found that targeted placement of cameras can double the detection probabilities of individuals. The advantages include increased estimate precision and accuracy, and the need for less sampling length or effort (Gerber and Parmenter, 2015). Still, the systematic layout yielded quite accurate estimates, and thus could be used in studies that have no effort to invest in the search of targeted locations, when the distribution of the chimpanzees under study is still unknown, or when trying to monitor several species at the same time. However, when chimpanzees are the focus of camera trap survey, a little extra effort should be invested to place the cameras in a way to maximize capture probabilities. With chimpanzees, this means placing them at frequently visited locations, such as trails, fruiting trees, natural bridges, and tool use sites. Tool use sites were especially good to obtain close-up videos of individuals, but not all individuals were filmed at those sites. However, cameras placed on trails or

bridges were able to capture the composition of different parties and all of the community travelling together.

1.5.4. Future development of camera traps as a survey method for great apes

Accurate density estimates are essential to assess the effects of specific threats, measure the success of management decisions and actions, and understand important aspects of a species' ecology. As a result, great ape conservation, ecology and sociodemography demand a good understanding of density, demographic trends, and distribution of great ape populations (Kühl *et al.*, 2008). Although camera trap studies incur high initial costs (Spehar *et al.*, 2015), they enable continuous data collection without the need of researchers being present, reducing the required sampling effort. Furthermore, cameras can monitor several species at the same time, making it possible to simultaneously study species richness and interspecies interactions while gathering census data (Klailova *et al.*, 2012; Boyer-Ontl and Pruetz, 2014). Head *et al.* (2013) and Boyer-Ontl and Pruetz (2014) were able to calculate sociodemographic structure from unhabituated chimpanzee groups with camera trap data, suggesting that there is potential for camera traps to monitor population dynamics on a long term basis (Head *et al.*, 2013). More specifically, Boyer-Ontl and Pruetz (2014) mention the advantage of using camera traps to collect data on vulnerable subjects such as females and their infants, as well as to monitor locations that are hard to access for researchers.

The results of this study emphasize the usability of camera trapping to monitor great ape populations. With high sampling effort and recapture rates, all capture-recapture models were able to yield accurate and precise density estimates. Thus, camera trapping is a robust and appropriate tool for the conservation ecology of primates.

1.6. CONCLUSION

This study emphasizes the suitability of combining C-R and SECR modeling and camera trapping as useful monitoring tools for great ape conservation. Although basic assumptions underlying C-R methods (e.g. population closure assumption) were not met, the results have shown that increasing the number of trapping occasions increases precision and accuracy of density estimates, but that there is a plateau in accuracy and precision around the 20th week under a targeted placement of cameras, and the 30th week under a systematic one. Capture probabilities will be maximized if cameras are placed at locations frequently visited by chimpanzees, which in turn increases precision and accuracy of estimates. However, a systematic layout also results in accurate estimates, and could be used in studies where chimpanzee distribution is unknown and no effort can be invested to find suitable targeted locations, or when trying to monitor several species at the same time.

Spatially explicit capture-recapture models have been extensively used to census populations of solitary species, mainly large carnivores (Gardner *et al.*, 2010; Obbard *et al.,* 2010; Royle *et al.,* 2011; Sollmann *et al.*, 2011; Gerber *et al.*, 2012; Gray and Prum, 2012; Noss *et al.*, 2012; Sollmann *et al.,* 2012; Blanc *et al,* 2013; Howe *et al.*, 2013; Tobler *et al.,* 2013; Rich *et al.,* 2014), and have only rarely been applied to studies on gregarious species (Head *et al.*, 2013; Moore and Vigilant, 2013; McCarthy *et al.*, 2015). I offer some insight on the use of SECR with gregarious and territorial species, by showing that violation of some basic assumptions in SECR does not affect the accuracy of their density estimates. As a result, I suggest that SECR models are chosen to estimate chimpanzee densities via camera traps, since they are able to include more sources of variation in capture probabilities, thereby reflecting known forms of uncertainty in density estimation. This emphasizes the suitability of camera trapping as a robust and appropriate tool for the conservation ecology of primates.

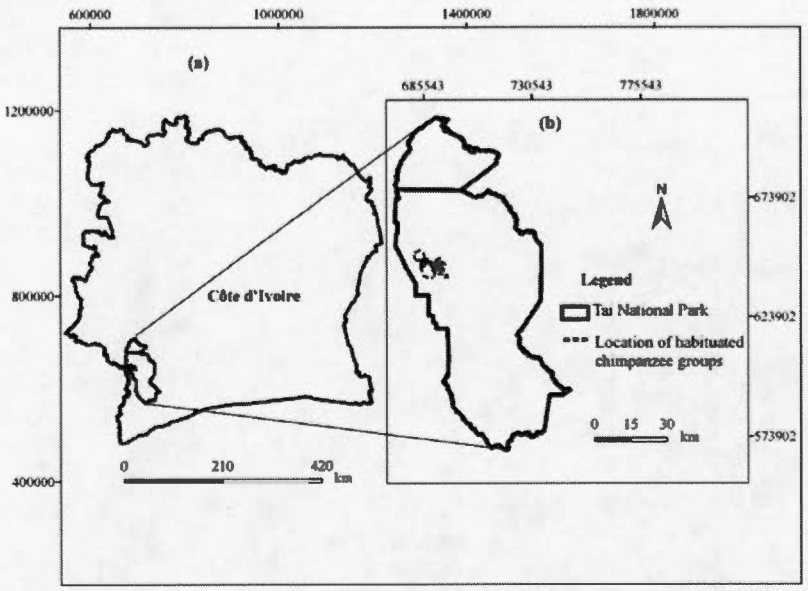

Figure 1.1 Map of the location of Taï National Park within Côte d'Ivoire (a), and the home ranges of the chimpanzee communities followed by the Taï Chimpanzee Project (TCP) (b). Home range of the east community is highlighted in red (modified version of map from Kouakou *et al.*, 2011).

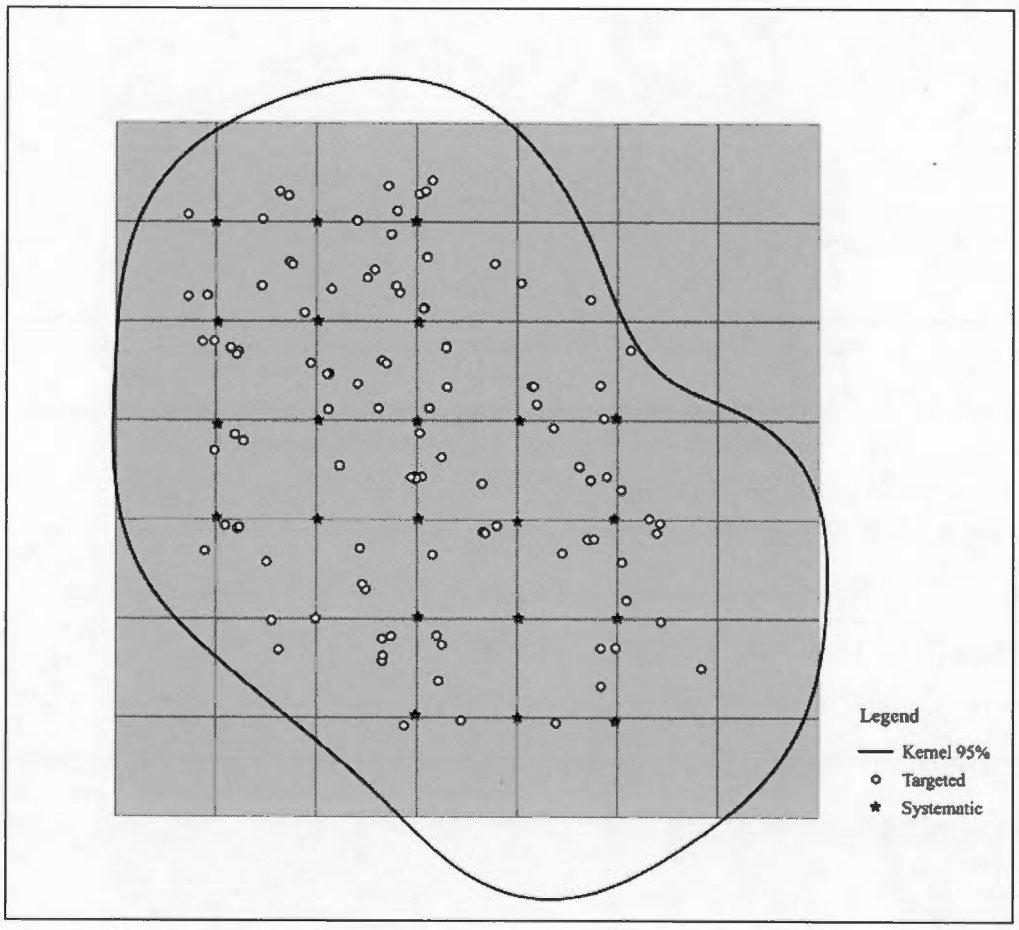

Figure 1.2 Locations of camera traps across the territory of the east community. The dark line represents the home range of the community as measured with the Kernel 95% method (total area of 40.37 km^2). Each cell of the grid is sized 1 x 1 km^2.

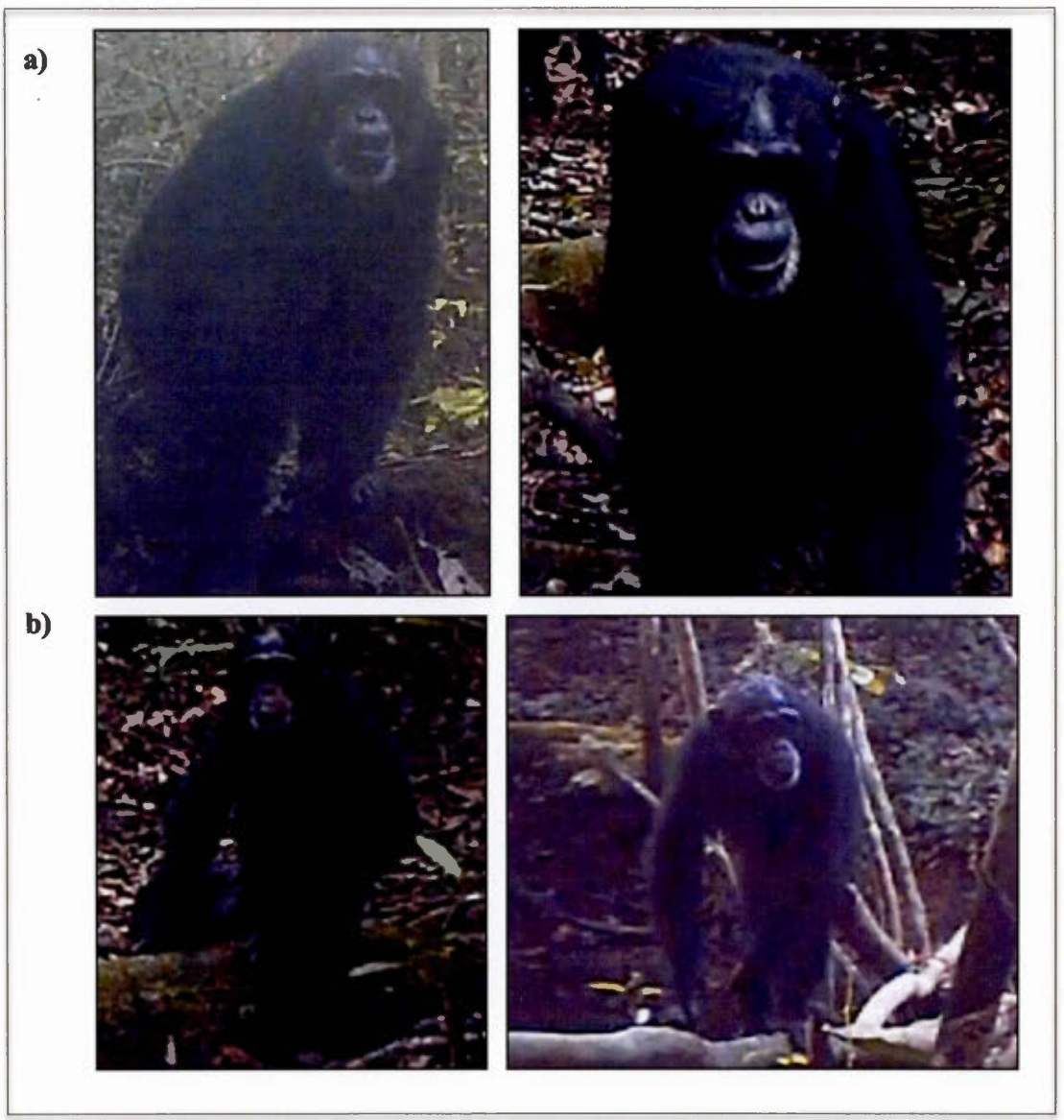

Figure 1.3 Example of identifications of individuals (a) Adult Male "Freddy", (b) Subadult female "Gia".

Table 1.1 Models fitted under each method to estimate density (see full description of each model under the appropriate sections: i, ii or iii).

(i.) Accumulation curve	(ii.) CAPTURE	(ii.) MARK	(iii.) SECR
Kohn estimator (Kohn *et al.*, 1999)	M_o*	M_o	*nullmodelt*
Eggert estimator (Eggert *et al.*, 2003)	M_h	M_h	*hmodel*
Bortz estimator (Bortz *et al.*, 1990)	M_b	M_b	*bmodel*
-	M_t	M_t	*tmodel*
-	M_{tb}	M_{tb}	*bkmodel*
-	Chao's (1989) M_t	-	-
-	Chao's (1988) M_h	-	-
-	Chao's *et al.* (1992) M_{th}	M_{th}	-
-	Population estimation with removal estimator	-	-
-	-	M_{tbh}	-
-	-	-	*hsexmodel*
-	-	-	*hagemodel*
-	-	-	*nullmodel***

** All subscripts or prefixes of model names represent the sources of variation considered in the model. (o): no variation in capture probability among individuals; (h): variation within individuals; (b): behavioural response to capture; (t): with time; (sex): between sexes; (age): between age classes; (bk) trap-specific response; or with a combination of these factors (h, bh, th).*

*** All SECR models, except the nullmodel, include variation in trapping effort (see section iii).*

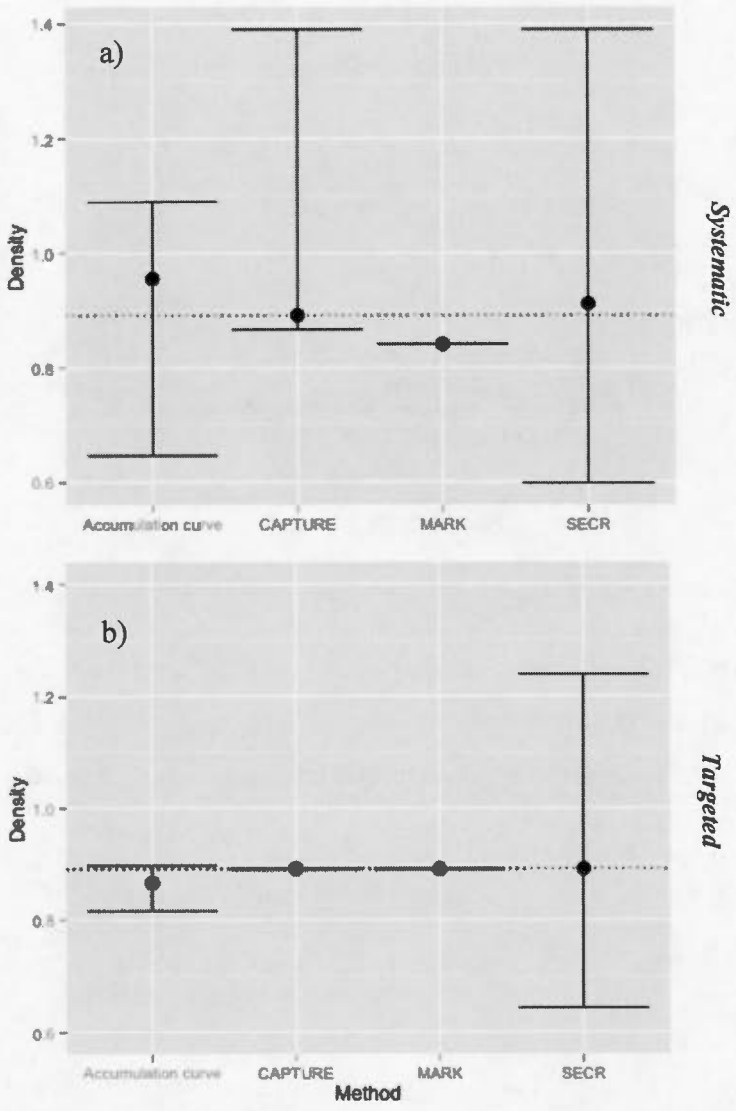

Figure 1.4 Density estimates and confidence intervals for best models under each method. (a) systematic layout, (b) targeted layout. The dotted lines represent the known density (D = 0.89 ind/km^2).

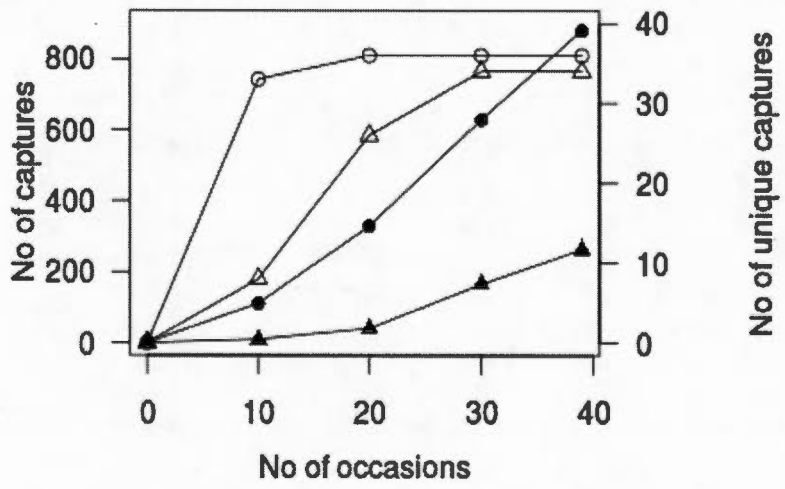

Figure 1.5 Number of captures (black) and unique individuals captured (white) caught for various occasion numbers. Triangles represent systematic data, dots targeted data.

Table 1.2 Density estimates, %CI and %Bias for best estimators under each condition (layout (S: systematic, T: targeted), number of trapping occasions, method). Most accurate estimates for each method are shown in bold and are represented in figure 1.4.*

Method	Layout	No Occ.	Model	D	% CI	% Bias
Acc. curve	S	10	-**	-	-	-
Acc. curve	S	20	Kohn	0.204	1762	77
Acc. curve	S	30	Kohn	0.606	534	32.0
Acc. curve	**S**	**39**	**Bortz**	**0.956**	**46.1**	**-7.16**
Acc. curve	T	10	Kohn	0.708	371	20.6
Acc. curve	**T**	**20**	**Bortz**	**0.888**	**29.7**	**0.422**
Acc. curve	T	30	Eggert	0.835	10.3	6.40
Acc. curve	T	38	Eggert	0.867	9.42	2.76
CAPTURE	S	10	M(th)	0.867	526	2.77
CAPTURE	S	20	M(h)	0.867	77.1	2.77
CAPTURE	S	30	M(h)	0.867	28.6	2.77
CAPTURE	**S**	**39**	**M(h)**	**0.892**	**58.3**	**-0.006**
CAPTURE	T	10	M(o)	0.867	22.9	2.77
CAPTURE	**T**	**20**	**M(t)**	**0.892**	**0**	**-0.006**
CAPTURE	T	**30**	**M(h); M(t)**	**0.892**	**0**	**-0.006**
CAPTURE	T	**38**	**M(h); M(t)**	**0.892**	**0**	**-0.006**
MARK	S	10	Mo	0.736	468	17.5
MARK	S	20	Mth	0.955	79.4	-7.10
MARK	S	**30**	**Mh**	**0.842**	**0.00**	**5.55**
MARK	**S**	**39**	**Mt; Mtb**	**0.842**	**0.00**	**5.55**
MARK	T	10	Mth	0.891	32.4	0.039
MARK	**T**	**20**	**Mo**	**0.892**	**0**	**-0.006**
MARK	T	**30**	**Mo; Mb**	**0.892**	**0**	**-0.006**
MARK	T	**38**	**Mt**	**0.892**	**0**	**-0.006**
SECR	S	10	*null*	0.665	367	25.5
SECR	S	20	*null*	1.06	101	-18.9
SECR	S	30	*bk*	0.856	68.5	4.02
SECR	**S**	**39**	***h***	**0.912**	**86.8**	**-2.30**
SECR	T	10	*b*	0.901	71.5	-1.02
SECR	**T**	20	*null*	0.892	66.5	-0.06
SECR	T	**30**	***nullt; t; bk; null***	**0.892**	**66.5**	**-0.05**
SECR	T	**38**	***nullt; t; bk***	**0.892**	**66.5**	**-0.05**

Results from all models from each method are presented in Appendix II.* * Number of recaptures (n=1) was too low under this condition. As a result, no estimate could be calculated.*

CONCLUSION GÉNÉRALE

La situation des grands singes est critique: si elle ne se sont pas déjà éteintes, la plupart des populations sauvages sont menacées de s'éteindre dans les prochaines années. Afin d'éviter ce déclin, les plans d'action de conservation visent, entre autres, à mettre en place des programmes de suivi à long terme pour identifier les zones d'action prioritaires, déterminer le statut UICN des espèces, et suivre les tendances dans la dynamique des populations (Kühl *et al.*, 2008; Maldonado *et al.*, 2012). Pour ce, il est nécessaire d'identifier des méthodes d'inventaire applicables à grande échelle, comparables entre sites et saisons. Pourtant, les études de validation des méthodes de suivi des populations de grands singes sont rares, voir inexistantes. Dans ce mémoire, je présente une des premières études de validation de technique d'inventaire de grands singes réalisées à ce jour.

Les inventaires de grands singes sont principalement réalisés par comptage de nids sur des transects linéaires, mais cette méthode nécessite une connaissance du taux de décomposition des matières végétales composant les nids, ainsi que du taux de production de nids par individu, des indices qui varient de site en site et de saison en saison (Kühl *et al.*, 2008). Récemment, les inventaires par échantillonnage génétique ont montré de bons progrès dans l'estimation des densités de grands singes. Les individus peuvent facilement être distingués les uns des autres, et ce, sans même devoir capturer ou observer les individus (Arandjelovic *et al.*, 2010). Pourtant, aucune étude de validation n'a encore été effectuée à ce jour.

Les caméras de piégeage sont de plus en plus utilisées dans le suivi des populations de grands singes. Head *et al.* (2012, 2013) ont pu calculer la distribution, la densité et la structure sociodémographique des chimpanzés et des gorilles au Gabon. Boyer-

Ontl et Pruetz (2014) ont pu étudier le comportement de chimpanzés non habitués au Sénégal, et Spehar *et al.* (2015) ont pu estimer la densité de populations d'orang-outan dans la forêt de Wehea, en Indonésie. Malgré cela, ici encore, aucune étude de validation n'a été réalisée, et les auteurs doivent se baser sur des estimations issues des méthodes de recensement conventionnelles pour estimer la validité des caméras.

Afin de savoir si les caméras de piégeage peuvent être utilisées dans le suivi des populations de chimpanzés, j'ai réalisé une étude de validation de la méthode sur le territoire d'une communauté de chimpanzés habituée à la présence humaine, et donc où la densité est connue. Pour ce faire, j'ai récolté des données vidéo issues de 81 caméras installées sur un territoire couvrant une aire de 42 km^2 pendant une période de 10 mois. Les caméras furent installées selon deux dispositions: un placement systématique, où les caméras étaient installées à tous les kilomètres, et un placement stratégique, où elles étaient placées à des endroits fréquemment visités par les chimpanzés.

Les résultats de cette étude ont montré que la méthode des caméras de piégeage peut être implémentée dans les programmes de suivi à long terme. Si les taux de détection sont élevés, les modèles de capture-recapture et de capture-recapture spatialement explicite donnent des estimations de densité très exactes de même que très précises. Même si un placement stratégique augmente les chances de filmer les chimpanzés, et ainsi la précision et l'exactitude des estimations, un placement systématique donne également des résultats satisfaisants. Lorsque les moyens sont limités, tant au niveau du matériel que du temps disponible, ou lorsque l'on veut surveiller plusieurs espèces à la fois, aucun effort n'est investi dans la recherche d'endroits qui augmentent les chances de filmer les chimpanzés. Les résultats ont alors montré qu'en plaçant les caméras de façon systématique, les modèles donnent des estimations exactes et précises.

Les modèles spatialement explicites de capture-recapture (SECR) ont largement été utilisés pour le recensement d'espèces solitaires, principalement avec les grands carnivores (Gardner *et al.*, 2010; Obbard *et al.*, 2010; Royle *et al.*, 2011; Sollmann *et al.*, 2011; Gerber *et al.*, 2012; Gray et Prum, 2012; Noss *et al.*, 2012; Sollmann *et al.*, 2012; Blanc *et al.*, 2013; Howe *et al.*, 2013; Tobler *et al.*, 2013; Rich *et al.*, 2014), et n'ont que rarement été appliqués aux études sur les espèces grégaires (Head *et al.*, 2013; Moore et Vigilant, 2013; McCarthy *et al.*, 2015). J'offre ici un aperçu de l'utilisation des modèles SECR avec des espèces grégaires et territoriales, en montrant que la violation de certaines hypothèses de base des modèles SECR n'affecte pas l'exactitude de leurs estimations de densité. Par conséquent, je suggère que les modèles SECR soient choisis pour estimer les densités de chimpanzés par caméras de piégeage, car ils sont en mesure d'inclure plus de sources de variation dans les probabilités de capture, reflétant ainsi de façon plus exacte les formes d'incertitude connues dans l'estimation des densités.

Bien que cette étude ait validé l'utilisation des modèles SECR, il y a un besoin pour développer des modèles qui tiennent compte des processus biologiques et comportementaux des espèces animales, tels que les interactions attractives et répulsives entre les individus causées par la territorialité et la socialité. De plus, les études de validation des méthodes de suivi des populations de grands singes restent rares, et ce malgré leur importance fondamentale dans l'amélioration des décisions de conservation. Ainsi, d'autres études de validation des méthodes de suivi doivent être réalisées sur des populations habituées, afin d'améliorer la pertinence des inventaires réalisés, et guider de façon appropriée la conservation des populations de grands singes.

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APPENDIX I - Individual capture histories and proportion of total captures

ID	Sex	Age	Systematic		Targeted	
			Nb of capt	% of total	Nb of capt	% of total
Athos	M	A	10	4.39	25	4.42
Bamou's baby	M	I	0	0	1	0.18
Bamou	F	A	0	0	1	0.18
Beatrice	F	J	7	3.07	22	3.89
Chantal	F	A	9	3.95	13	2.30
Cherry	F	I	9	3.95	13	2.30
Elisa	F	A	6	2.63	14	2.48
Emma	F	I	6	2.63	13	2.30
Eolos	M	J	6	2.63	25	4.42
Erasmus	M	J	7	3.07	13	2.30
Fatima	F	A	6	2.63	20	3.54
Fiesta	M	I	6	2.63	20	3.54
Fredy	M	A	6	2.63	22	3.89
Gia	F	S	3	1.32	12	2.12
Indira	F	A	7	3.07	22	3.89
Ivoire	M	I	7	3.07	22	3.89
Karibou	F	I	7	3.07	13	2.30
Korie	F	A	7	3.07	13	2.30
Kosmos	F	J	2	0.88	5	0.88
Maïmouna	F	J	6	2.63	19	3.36
Pessoa	M	J	8	3.51	15	2.65
Placali	F	I	8	3.51	17	3.01
Pola	F	A	8	3.51	17	3.01
Poseidon	M	A	10	4.39	17	3.01
Quarantaine	F	J	9	3.95	19	3.36
Repos	M	J	9	3.95	20	3.54
Richelieu	M	A	10	4.39	22	3.89
Rwanda	F	I	10	4.39	17	3.01
Rwenzori	F	A	10	4.39	17	3.01
Wandy	F	A	5	2.19	14	2.48
Weh	M	J	1	0.44	10	1.77
Willy	M	A	7	3.07	22	3.89
Woloso	F	S	1	0.44	3	0.53
Yeda	F	S	7	3.07	21	3.72
Yeha	F	A	4	1.75	13	2.30
Yoyo	M	J	4	1.75	13	2.30
Sum			228	100	565	100
Mean			6	2.78	16	2.78
Min.			0	0	1	0.177
Max.			10	4.39	25	4.42

APPENDIX II - Population size, density estimates and their respective standard errors and 95% confidence intervals given by each method (Accumulation curves, CAPTURE, MARK, SECR)*

Method	Model	Design	k	n	No of ind. captured	Total no of captures	*D*	SE	CI_L	CI_U	%CI	%Bias
ACC_CURVES	Kohn	S	10	23	8	9	-	-	-	-	-	-
ACC_CURVES	Eggert	S	10	23	8	9	-	-	-	-	-	-
ACC_CURVES	Bortz	S	10	23	8	9	-	-	-	-	-	-
ACC_CURVES	**Kohn**	**S**	**20**	**23**	**26**	**39**	**0,204**	**-**	**0,175**	**3,77**	**1762**	**77**
ACC_CURVES	Eggert	S	20	23	26	39	0,153	-	0,135	1,88	1136	82,8
ACC_CURVES	Bortz	S	20	23	26	39	0,148	-	0,125	0,835	481	83,5
ACC_CURVES	**Kohn**	**S**	**30**	**23**	**34**	**142**	**0,606**	**-**	**0,542**	**3,78**	**534**	**32**
ACC_CURVES	Eggert	S	30	23	34	142	0,527	-	0,462	2,01	293	40,9
ACC_CURVES	Bortz	S	30	23	34	142	0,543	-	0,447	1,59	210	39,1
ACC_CURVES	Kohn	S	39	23	34	228	1,55	-	0,726	1,77	67,2	-73,9
ACC_CURVES	Eggert	S	39	23	34	228	1,04	-	0,652	1,18	50,8	-16,2
ACC_CURVES	**Bortz**	**S**	**39**	**23**	**34**	**228**	**0,956**	**-**	**0,647**	**1,09**	**46,1**	**-7,16**
ACC_CURVES	**Kohn**	**T**	**10**	**58**	**33**	**81**	**0,708**	**-**	**0,572**	**3,20**	**371**	**20,6**
ACC_CURVES	Eggert	T	10	58	33	81	0,610	-	0,459	1,75	212	31,6
ACC_CURVES	Bortz	T	10	58	33	81	1,89	-	0,454	2,02	82,7	-112
ACC_CURVES	Kohn	T	20	58	36	218	0,935	-	0,843	1,24	42	-4,87
ACC_CURVES	Eggert	T	20	58	36	218	0,874	-	0,760	0,944	21	1,98
ACC_CURVES	**Bortz**	**T**	**20**	**58**	**36**	**218**	**0,888**	**-**	**0,779**	**1,04**	**29,7**	**0,422**
ACC_CURVES	Kohn	T	30	58	36	391	0,964	-	0,854	1,06	21,6	-8,13
ACC_CURVES	**Eggert**	**T**	**30**	**58**	**36**	**391**	**0,835**	**-**	**0,820**	**0,906**	**10,3**	**6,40**
ACC_CURVES	Bortz	T	30	58	36	391	0,822	-	0,826	0,909	10,1	7,80
ACC_CURVES	Kohn	T	38	58	36	565	0,961	-	0,846	1,01	16,9	-7,76
ACC_CURVES	**Eggert**	**T**	**38**	**58**	**36**	**565**	**0,867**	**-**	**0,817**	**0,898**	**9,42**	**2,76**
ACC_CURVES	Bortz	T	38	58	36	565	0,863	-	0,821	0,903	9,55	3,20
CAPTURE	M(o)	S	10	23	8	9	0,743	0,617	0,297	3,42	420	16,7
CAPTURE	M(h)	S	10	23	8	9	0,471	0,175	0,297	1,04	158	47,2
CAPTURE	M(b)	S	10	23	8	9	-	-	-	-	-	-
CAPTURE	M(t)	S	10	23	8	9	0,595	0,427	0,272	2,40	358	33,3
CAPTURE	**M(th) - Chao *et al.* (1992)**	**S**	**10**	**23**	**8**	**9**	**0,867**	**0,863**	**0,297**	**4,86**	**526**	**2,77**
CAPTURE	M(tb)	S	10	23	8	9	-	-	-	-	-	-
CAPTURE	M(t) - Chao (1989)	S	10	23	8	9	0,421	0,231	0,248	1,39	271	52,8
CAPTURE	M(h) - Chao (1988)	S	10	23	8	9	0,817	0,771	0,297	4,34	494	8,33
CAPTURE	Population estimation with removal estimator	S	10	23	8	9	0,421	0,235	0,248	1,39	271	52,8
CAPTURE	M(o)	S	20	23	26	39	1,04	0,202	0,817	1,63	78,6	-16,7
CAPTURE	M(h)	S	20	23	26	39	0,917	0,134	0,768	1,31	59,5	-2,78
CAPTURE	M(b)	S	20	23	26	39	-	-	-	-	-	-
CAPTURE	M(t)	S	20	23	26	39	0,966	0,164	0,768	1,46	71,8	-8,34

CAPTURE	M(th) - Chao *et al.* (1992)	S	20	23	26	39	0,966	0,174	0,768	1,49	74,4	-8,34
CAPTURE	M(tb)	S	20	23	26	39	1,09	0	1,09	1,09	0	-22,2
CAPTURE	M(t) - Chao (1989)	S	20	23	26	39	0,817	0,117	0,694	1,21	63,6	8,33
CAPTURE	**M(h) - Chao (1988)**	**S**	**20**	**23**	**26**	**39**	**0,867**	**0,154**	**0,718**	**1,39**	**77,1**	**2,77**
CAPTURE	Population estimation with removal estimator	S	20	23	26	39	0,644	0	0,644	0,644	0	27,8
CAPTURE	M(o)	S	30	23	34	142	0,842	0,016	0,842	0,842	0	5,55
CAPTURE	M(h)	S	30	23	34	142	0,941	0,076	0,892	1,21	34,2	-5,56
CAPTURE	M(b)	S	30	23	34	142	3,99	9,02	1,02	59,2	1458	-347
CAPTURE	M(t)	S	30	23	34	142	0,842	0	0,842	0,842	0	5,55
CAPTURE	M(th) - Chao *et al.* (1992)	S	30	23	34	142	0,842	0,019	0,842	0,941	11,8	5,55
CAPTURE	M(tb)	S	30	23	34	142	0,842	0	0,842	0,842	0	5,55
CAPTURE	M(t) - Chao (1989)	S	30	23	34	142	0,842	0	0,842	0,842	0	5,55
CAPTURE	**M(h) - Chao (1988)**	**S**	**30**	**23**	**34**	**142**	**0,867**	**0,046**	**0,867**	**1,11**	**28,6**	**2,77**
CAPTURE	Population estimation with removal estimator	S	30	23	34	142	0,842	0	0,842	0,842	0	5,55
CAPTURE	M(o)	S	39	23	34	228	0,842	0,004	0,842	0,842	0	5,55
CAPTURE	M(h)	S	39	23	34	228	0,941	0,053	0,892	1,09	21,1	-5,56
CAPTURE	M(b)	S	39	23	34	228	1,02	0,153	0,892	1,61	70,7	-13,9
CAPTURE	M(t)	S	39	23	34	228	0,842	0	0,842	0,842	0	5,55
CAPTURE	M(th) - Chao *et al.* (1992)	S	39	23	34	228	0,842	0,019	0,842	0,941	11,8	5,55
CAPTURE	M(tb)	S	39	23	34	228	0,842	0	0,842	0,842	0	5,55
CAPTURE	M(t) - Chao (1989)	S	39	23	34	228	0,842	0	0,842	0,842	0	5,55
CAPTURE	**M(h) - Chao (1988)**	**S**	**39**	**23**	**34**	**228**	**0,892**	**0,092**	**0,867**	**1,39**	**58,3**	**-0,006**
CAPTURE	Population estimation with removal estimator	S	39	23	34	228	0,842	0	0,842	0,842	0	5,55
CAPTURE	**M(o)**	**T**	**10**	**58**	**33**	**81**	**0,867**	**0,047**	**0,842**	**1,04**	**22,9**	**2,77**
CAPTURE	M(h)	T	10	58	33	81	1,09	0,152	0,917	1,56	59,1	-22,2
CAPTURE	M(b)	T	10	58	33	81	-	-	-	-	-	-
CAPTURE	M(t)	T	10	58	33	81	0,842	0,029	0,842	0,966	14,7	5,55
CAPTURE	M(th) - Chao *et al.* (1992)	T	10	58	33	81	1,09	0,169	0,917	1,63	65,9	-22,2
CAPTURE	M(tb)	T	10	58	33	81	0,917	0	0,917	0,917	0	-2,78
CAPTURE	M(t) - Chao (1989)	T	10	58	33	81	1,02	0,144	0,892	1,51	61	-13,9
CAPTURE	M(h) - Chao (1988)	T	10	58	33	81	1,11	0,218	0,917	1,88	86,7	-25
CAPTURE	Population estimation with removal estimator	T	10	58	33	81	1,71	0,47	1,16	3,17	117	-91,7
CAPTURE	M(o)	T	20	58	36	218	0,892	0,004	0,892	0,892	0	-0,006
CAPTURE	M(h)	T	20	58	36	218	0,991	0,05	0,941	1,14	20	-11,1
CAPTURE	M(b)	T	20	58	36	218	0,917	0,043	0,917	1,14	24,3	-2,78
CAPTURE	M(t)	T	20	58	36	218	0,892	0	0,892	0,892	0	-0,006
CAPTURE	M(th) - Chao *et al.* (1992)	-T	20	58	36	218	0,917	0,024	0,917	1,02	10,8	-2,78

CAPTURE	M(tb)	T	20	58	36	218	0,892	0,005	0,892	0,892	0	-0,006
CAPTURE	**M(t) - Chao (1989)**	**T**	**20**	**58**	**36**	**218**	**0,892**	**0**	**0,892**	**0,892**	**0**	**-0,006**
CAPTURE	M(h) - Chao (1988)	T	20	58	36	218	0,941	0,093	0,917	1,44	55,3	-5,56
CAPTURE	Population estimation with removal estimator	T	20	58	36	218	0,892	0	0,892	0,892	0	-0,006
CAPTURE	M(o)	T	30	58	36	391	0,892	0	0,892	0,892	0	-0,006
CAPTURE	M(h)	T	30	58	36	391	0,991	0,072	0,941	1,24	30	-11,1
CAPTURE	M(b)	T	30	58	36	391	0,892	0,012	0,892	0,892	0	-0,006
CAPTURE	M(t)	T	30	58	36	391	0,892	0	0,892	0,892	0	-0,006
CAPTURE	M(th) - Chao *et al.* (1992)	T	30	58	36	391	0,892	0,019	0,892	0,991	11,1	-0,006
CAPTURE	M(tb)	T	30	58	36	391	0,892	0	0,892	0,892	0	-0,006
CAPTURE	**M(t) - Chao (1989)**	**T**	**30**	**58**	**36**	**391**	**0,892**	**0**	**0,892**	**0,892**	**0**	**-0,006**
CAPTURE	**M(h) - Chao (1988)**	**T**	**30**	**58**	**36**	**391**	**0,892**	**0**	**0,892**	**0,892**	**0**	**-0,006**
CAPTURE	Population estimation with removal estimator	T	30	58	36	391	0,892	0	0,892	0,892	0	-0,006
CAPTURE	M(o)	T	38	58	36	565	0,892	0	0,892	0,892	0	-0,006
CAPTURE	M(h)	T	38	58	36	565	0,991	0,078	0,941	1,26	32,5	-11,1
CAPTURE	M(b)	T	38	58	36	565	0,892	0	0,892	0,892	0	-0,006
CAPTURE	M(t)	T	38	58	36	565	0,892	0	0,892	0,892	0	-0,006
CAPTURE	M(th) - Chao *et al.* (1992)	T	38	58	36	565	0,892	0,018	0,892	0,991	11,1	-0,006
CAPTURE	M(tb)	T	38	58	36	565	0,892	0	0,892	0,892	0	-0,006
CAPTURE	**M(t) - Chao (1989)**	**T**	**38**	**58**	**36**	**565**	**0,892**	**0**	**0,892**	**0,892**	**0**	**-0,006**
CAPTURE	**M(h) - Chao (1988)**	**T**	**38**	**58**	**36**	**565**	**0,892**	**0**	**0,892**	**0,892**	**0**	**-0,006**
CAPTURE	Population estimation with removal estimator	T	38	58	36	565	0,892	0	0,892	0,892	0	-0,006
MARK	**M(o)**	**S**	**10**	**23**	**8**	**9**	**0,736**	**0,660**	**0,280**	**3,72**	**468**	**17,5**
MARK	M(t)	S	10	23	8	9	0,600	0,512	0,257	2,95	450	32,8
MARK	M(b)	S	10	23	8	9	0,263	0,150	0,203	1,13	352	70,5
MARK	M(h)	S	10	23	8	9	0,736	0,660	0,280	3,72	468	17,5
MARK	M(th)	S	10	23	8	9	0,600	0,512	0,257	2,95	450	32,8
MARK	M(tb)	S	10	23	8	9	0,198	0	0,198	0,198	0,00	77,8
MARK	M(tbh)	S	10	23	8	9	0,198	0	0,198	0,198	0,00	77,8
MARK	M(o)	S	20	23	26	39	1,03	0,205	0,791	1,67	85,3	-15,7
MARK	M(t)	S	20	23	26	39	0,955	0,175	0,755	1,51	79,4	-7,10
MARK	M(b)	S	20	23	26	39	1233	35013	8,37	196416	15933	-138133
MARK	M(h)	S	20	23	26	39	1,03	0,205	0,791	1,67	85,3	-15,7
MARK	**M(th)**	**S**	**20**	**23**	**26**	**39**	**0,955**	**0,175**	**0,755**	**1,51**	**79,4**	**-7,10**
MARK	M(tb)	S	20	23	26	39	0,644	0	0,644	0,644	0,00	27,8
MARK	M(tbh)	S	20	23	26	39	0,644	0	0,644	0,644	0,00	27,8
MARK	M(o)	S	30	23	34	142	0,842	0	0,842	0,842	0,00	5,55
MARK	M(t)	S	30	23	34	142	0,842	0	0,842	0,842	0,00	5,55
MARK	M(b)	S	30	23	34	142	1,77	1,21	0,973	7,40	364	-98,2

MARK	**M(h)**	**S**	**30**	**23**	**34**	**142**	**0,842**	**0**	**0,842**	**0,842**	**0,00**	**5,55**
MARK	M(th)	S	30	23	34	142	0,842	0	0,842	0,842	0,00	5,55
MARK	M(tb)	S	30	23	34	142	0,842	0	0,842	0,842	0,00	5,55
MARK	M(tbh)	S	30	23	34	142	0,842	0	0,842	0,842	0,00	5,55
MARK	M(o)	S	39	23	34	228	0,842	0	0,842	0,842	0,00	5,55
MARK	**M(t)**	**S**	**39**	**23**	**34**	**228**	**0,842**	**0**	**0,842**	**0,842**	**0,00**	**5,55**
MARK	M(b)	S	39	23	34	228	0,944	0,103	0,862	1,37	53,8	-5,81
MARK	M(h)	S	39	23	34	228	0,842	0	0,842	0,842	0,00	5,55
MARK	M(th)	S	39	23	34	228	0,842	0	0,842	0,842	0,00	5,55
MARK	**M(tb)**	**S**	**39**	**23**	**34**	**228**	**0,842**	**0**	**0,842**	**0,842**	**0,00**	**5,55**
MARK	M(tbh)	S	39	23	34	228	0,842	0	0,842	0,842	0,00	5,55
MARK	M(o)	T	10	58	33	81	0,851	0,039	0,823	1,02	23,7	4,55
MARK	M(t)	T	10	58	33	81	0,837	0,032	0,819	1,00	21,9	6,17
MARK	M(b)	T	10	58	33	81	1,19	0,369	0,889	2,71	153	-33,0
MARK	M(h)	T	10	58	33	81	0,851	0,039	0,823	1,02	23,7	4,55
MARK	**M(th)**	**T**	**10**	**58**	**33**	**81**	**0,891**	**0,062**	**0,835**	**1,12**	**32,4**	**0,039**
MARK	M(tb)	T	10	58	33	81	0,817	0	0,817	0,817	0,00	8,33
MARK	M(tbh)	T	10	58	33	81	0,817	0	0,817	0,817	0,00	8,33
MARK	**M(o)**	**T**	**20**	**58**	**36**	**218**	**0,892**	**0**	**0,892**	**0,892**	**0,00**	**-0,006**
MARK	M(t)	T	20	58	36	218	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(b)	T	20	58	36	218	0,892	0	0,892	0,892	0,07	-0,006
MARK	M(h)	T	20	58	36	218	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(th)	T	20	58	36	218	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(tb)	T	20	58	36	218	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(tbh)	T	20	58	36	218	0,892	0	0,892	0,892	0,00	-0,006
MARK	**M(o)**	**T**	**30**	**58**	**36**	**391**	**0,892**	**0**	**0,892**	**0,892**	**0,00**	**-0,006**
MARK	M(t)	T	30	58	36	391	0,892	0	0,892	0,892	0,00	-0,006
MARK	**M(b)**	**T**	**30**	**58**	**36**	**391**	**0,892**	**0**	**0,892**	**0,892**	**0,00**	**-0,006**
MARK	M(h)	T	30	58	36	391	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(th)	T	30	58	36	391	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(tb)	T	30	58	36	391	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(tbh)	T	30	58	36	391	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(o)	T	38	58	36	565	0,892	0	0,892	0,892	0,00	-0,006
MARK	**M(t)**	**T**	**38**	**58**	**36**	**565**	**0,892**	**0**	**0,892**	**0,892**	**0,00**	**-0,006**
MARK	M(b)	T	38	58	36	565	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(h)	T	38	58	36	565	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(th)	T	38	58	36	565	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(tb)	T	38	58	36	565	0,892	0	0,892	0,892	0,00	-0,006
MARK	M(tbh)	T	38	58	36	565	0,892	0	0,892	0,892	0,00	-0,006
SECR	nullmodel	S	10	23	8	10	0,657	0,523	0,167	2,59	369	26,3
SECR	hsex	S	10	23	8	10	0,598	0,738	0,053	6,42	1065	33,0
SECR	hage	S	10	23	8	10	-	-	-	-	-	-
SECR	tmodel	S	10	23	8	10	0,645	0,500	0,168	2,48	358	27,7

SECR	h2model	S	10	23	8	10	0,657	0,523	0,167	2,59	369	26,3
SECR	bmodel	S	10	23	8	10	0,318	0,248	0,082	1,23	360	64,3
SECR	bkmodel	S	10	23	8	10	0,620	0,476	0,164	2,35	353	30,4
SECR	**nullmodelt**	**S**	**10**	**23**	**8**	**10**	**0,665**	**0,526**	**0,169**	**2,61**	**367**	**25,5**
SECR	nullmodel	S	20	23	26	40	1,07	0,271	0,655	1,74	102	-19,9
SECR	hsex	S	20	23	26	40	1,06	0,264	0,657	1,72	100	-19,0
SECR	hage	S	20	23	26	40	1,79	5,54	0,089	36,3	2017	-101
SECR	tmodel	S	20	23	26	40	1,06	0,266	0,650	1,72	101	-18,5
SECR	h2model	S	20	23	26	40	1,07	0,271	0,655	1,74	102	-19,9
SECR	bmodel	S	20	23	26	40	2,61	2,57	0,520	13,1	481	-193
SECR	bkmodel	S	20	23	26	40	1,13	0,303	0,677	1,90	108	-27,0
SECR	**nullmodelt**	**S**	**20**	**23**	**26**	**40**	**1,06**	**0,267**	**0,652**	**1,72**	**101**	**-18,9**
SECR	nullmodel	S	30	23	34	165	0,849	0,147	0,607	1,19	68,5	4,75
SECR	hsex	S	30	23	34	165	0,849	0,146	0,608	1,19	68,0	4,74
SECR	hage	S	30	23	34	165	0,854	0,147	0,611	1,19	68,1	4,28
SECR	tmodel	S	30	23	34	165	0,849	0,147	0,607	1,19	68,5	4,77
SECR	h2model	S	30	23	34	165	0,849	0,147	0,607	1,19	68,5	4,75
SECR	bmodel	S	30	23	34	165	1,58	0,747	0,657	3,81	199	-77,4
SECR	**bkmodel**	**S**	**30**	**23**	**34**	**165**	**0,856**	**0,148**	**0,611**	**1,20**	**68,5**	**4,02**
SECR	nullmodelt	S	30	23	34	165	0,849	0,147	0,607	1,19	68,5	4,74
SECR	nullmodel	S	39	23	34	263	0,843	0,146	0,602	1,18	68,5	5,47
SECR	hsex	S	39	23	34	263	0,843	0,145	0,604	1,18	68	5,47
SECR	hage	S	39	23	34	263	0,843	0,145	0,604	1,18	68	5,41
SECR	tmodel	S	39	23	34	263	0,843	0,146	0,602	1,18	68,5	5,47
SECR	**h2model**	**S**	**39**	**23**	**34**	**263**	**0,912**	**0,198**	**0,599**	**1,39**	**86,8**	**-2,30**
SECR	bmodel	S	39	23	34	263	1,03	0,223	0,673	1,56	86,8	-15,0
SECR	bkmodel	S	39	23	34	263	0,845	0,146	0,604	1,18	68,5	5,23
SECR	nullmodelt	S	39	23	34	263	0,843	0,146	0,602	1,18	68,5	5,46
SECR	nullmodel	T	10	58	33	111	0,940	0,168	0,664	1,33	70,9	-5,40
SECR	hsex	T	10	58	33	111	0,965	0,173	0,681	1,37	71,1	-8,24
SECR	hage	T	10	58	33	111	0,955	0,171	0,675	1,35	70,9	-7,09
SECR	tmodel	T	10	58	33	111	0,941	0,168	0,665	1,33	70,8	-5,57
SECR	h2model	T	10	58	33	111	0,948	0,170	0,670	1,34	71,0	-6,34
SECR	**bmodel**	**T**	**10**	**58**	**33**	**111**	**0,901**	**0,162**	**0,635**	**1,28**	**71,5**	**-1,02**
SECR	bkmodel	T	10	58	33	111	0,964	0,174	0,679	1,37	71,7	-8,13
SECR	nullmodelt	T	10	58	33	111	0,934	0,167	0,660	1,32	70,8	-4,78
SECR	nullmodel	T	20	58	36	329	0,892	0,150	0,644	1,24	66,5	-0,07
SECR	hsex	T	20	58	36	329	0,892	0,149	0,645	1,23	66,0	-0,07
SECR	hage	T	20	58	36	329	0,892	0,149	0,645	1,23	66,0	-0,07
SECR	tmodel	T	20	58	36	329	0,892	0,150	0,644	1,24	66,5	-0,07
SECR	h2model	T	20	58	36	329	-	-	-	-	-	-
SECR	bmodel	T	20	58	36	329	0,894	0,150	0,645	1,24	66,5	-0,22
SECR	bkmodel	T	20	58	36	329	0,893	0,150	0,644	1,24	66,5	-0,10
SECR	**nullmodelt**	**T**	**20**	**58**	**36**	**329**	**0,892**	**0,150**	**0,644**	**1,24**	**66,5**	**-0,06**

SECR	**nullmodel**	**T**	**30**	**58**	**36**	**629**	**0,892**	**0,150**	**0,644**	**1,24**	**66,5**	**-0,05**
SECR	hsex	T	30	58	36	629	0,892	0,149	0,645	1,23	66,0	-0,06
SECR	hage	T	30	58	36	629	0,892	0,149	0,645	1,23	66,0	-0,06
SECR	**tmodel**	**T**	**30**	**58**	**36**	**629**	**0,892**	**0,150**	**0,644**	**1,24**	**66,5**	**-0,05**
SECR	h2model	T	30	58	36	629	-	-	-	-	-	-
SECR	bmodel	T	30	58	36	629	0,893	0,150	0,644	1,24	66,5	-0,14
SECR	**bkmodel**	**T**	**30**	**58**	**36**	**629**	**0,892**	**0,150**	**0,644**	**1,24**	**66,5**	**-0,05**
SECR	**nullmodelt**	**T**	**30**	**58**	**36**	**629**	**0,892**	**0,150**	**0,644**	**1,24**	**66,5**	**-0,05**
SECR	**nullmodel**	**T**	**38**	**58**	**36**	**881**	**0,892**	**0,150**	**0,644**	**1,24**	**66,5**	**-0,05**
SECR	hsex	T	38	58	36	881	-	-	-	-	-	-
SECR	hage	T	38	58	36	881	-	-	-	-	-	-
SECR	**tmodel**	**T**	**38**	**58**	**36**	**881**	**0,892**	**0,150**	**0,644**	**1,24**	**66,5**	**-0,05**
SECR	h2model	T	38	58	36	881	-	-	-	-	-	-
SECR	bmodel	T	38	58	36	881	0,893	0,150	0,644	1,24	66,5	-0,10
SECR	**bkmodel**	**T**	**38**	**58**	**36**	**881**	**0,892**	**0,150**	**0,644**	**1,24**	**66,5**	**-0,05**
SECR	nullmodelt	T	38	58	36	881	0,893	0,150	0,644	1,24	66,5	-0,10

* *S= systematic layout, T= targeted layout, k=number of occasions, n=number of cameras. Models with most accurate density estimates under each condition are in bold. In cases where no values are shown (-), models were not able to estimate density from the capture data, either because sample size was too small, or because of errors found by the R program in sampling the variance from the data.*

APPENDIX III - Results from the SECR function *mask.check*

Buffer size (m)*	ESA (m)	D (ind/km^2)	SE (ind/km^2)
systematic			
100	69,8	48,7	8,42
500	1725	1,97	0,340
1000	**3174**	**1,07**	**0,185**
2000	5717	0,595	0,102
5000	16873	0,202	0,0348
targeted			
100	275	13,1	2,20
500	2703	1,33	0,224
1000	**4047**	**0,890**	**0,149**
2000	0	8,49E+08	1,41E+08
5000	0	2,04E+07	-

**Most accurate density estimates under each layout are highlighted in bold. ESA = Effective sampling area, D: Density, SE: Standard Error of density estimate.*